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# Fishery Bulletin

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# Fishery Bulletin

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# Effects of Water Temperature on Size and Biochemical Composition of Winter Flounder *Pseudopleuronectes americanus* at Hatching and Feeding Initiation

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**Abstract.**—Winter flounder were acclimated to two temperatures (2° and 7°C) for a period of about 7 weeks prior to spawning. Embryos produced at two acclimation temperatures were incubated through the yolksac stage at three incubation temperatures (4°, 7°, and 10°C). Both adult acclimation temperature and embryo and larval incubation temperature were found to have an effect on larval size and biochemical composition. In many cases the effects of acclimation temperature and incubation temperature were nonadditive. RNA content at first feeding indicated that larvae produced by adults acclimated to low temperature (2°C) were better suited for growth at low temperatures, while larvae produced by adults acclimated to higher temperature (7°C) were better suited for growth at higher temperatures. At first feeding larvae were larger (higher standard length) and in better condition (high protein and RNA content) when incubated at lower temperatures.

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The effects of water temperature on the size and viability of fish eggs and larvae have been the subject of considerable interest. Water temperature is the environmental variable most often linked to recruitment in retrospective empirical analyses of recruitment variability in temperate marine fish (Sissenwine 1984). Yet in most cases causation is not established and the mechanisms involved are poorly understood. Studies of effects of water temperature prior to spawning suggest an inverse relation between water temperature and egg size in several species (Hempel and Blaxter 1967, Cushing 1967, Bagenal 1971, Southward and Demir 1974, Ware 1975, Tanasichuk and Ware 1987). The effects of water temperature during the embryonic period on larval size and yolk conversion efficiency have been examined in a variety of species (Lasker 1962, Sweet and Kinne 1964, Alderdice and Forrester 1968, May 1974, Laurence and Rogers 1976, Linden et al. 1980, Johns et al. 1981, Laurence and Howell 1981, Buckley et al. 1982). While maximum efficiency is generally achieved at intermediate temperatures within the range of thermal tolerance, the exact shape of the relation between temperature and utilization is variable (Heming and Buddington 1988). Blaxter and Hempel (1966) found that the effect of temperature on yolk conversion efficiency was dependent upon egg size in Atlantic herring *Clupea harengus*, cold temperatures favoring small eggs and warm temperatures favoring large eggs. The effects of water temperature have been examined in combination with salinity, oxygen levels, and other environmental variables. None of these studies, with the exception of Tanasichuk and Ware 1987, considered a possible interactive effect of water temperature during gamete maturation with water temperature during the embryonic and larval periods. It is widely known, however, that acclimation temperature mediates many thermal effects, including upper and lower lethal temperatures and metabolic rate (Brett 1970).

This study was undertaken to examine the effects of water temperature during the latter stages of gamete development and during the embryonic and yolksac periods on the size and biochemical composition of winter flounder larvae produced. Standard length, RNA, DNA, and protein content were determined at hatching and first feeding. These indices were chosen because of their relation to fitness, growth, and survival potential of fish larvae. Length

has been related to swimming speed and the ability to capture prey and avoid preditors (Folkvord and Hunter 1986, Miller et al. 1988). Bulk RNA content is primarily a measure of ribosomal RNA content which is an index of an organism's capacity for synthesis of protein and growth (Bulow 1987). DNA content is an index of cell number and developmental state. Protein, the primary organic constituent in fish larvae, is generally proportional to dry weight (Buckley 1979). Growth of fish larvae is primarily accomplished through protein synthesis and accumulation. Protein is also an important source of reserve energy during larval development (Buckley 1979).

The primary hypothesis tested was that water temperatures, both during gamete maturation and during embryonic and early larval development, and their interaction had an effect on the size and composition of larvae produced. It was reasoned that eggs produced by adults acclimated to low temperatures would be better adapted to low temperatures than eggs produced by adults acclimated to high temperatures. It was expected that the converse was true for eggs produced by adults acclimated to high temperatures. This study originated in part out of an earlier study indicating that winter flounder embryos produced at low temperature exhausted their yolk reserves prior to feeding initiation and appeared poorly suited for growth and survival when incubated and reared at higher temperatures (Buckley 1982). It is part of a larger study of the effects of parental and environmental factors on the size and viability of winter flounder eggs and larvae. The rationale for this larger effort is that given the high fecundity of temperate marine fishes and the high mortality rates during their early life stages, variability at the individual, brood and stock level in size and composition of fish eggs and larvae may play a large part in determining survival during the early life stages and consequently in determining recruitment success.

## Methods

Mature winter flounder were caught with an otter trawl on 23 December 1980 in the West Passage of Narragansett Bay in the vicinity of Fox Island at a water temperature of 3.5°C (Table 1). Fish were randomly assigned to two groups (acclimation temperatures). One was held at 2°C, the other at 7°C. Spawning was induced by injections of carp pituitary extract administered as described by Smigielski (1975). Eggs were stripped, fertilized with the sperm of three males held at the same temperature as the spawning female, and treated with diatomaceous earth (Smigielski and Arnold 1972). Embryos from each female were randomly split into three groups of about 1500 each and incubated at 4°, 7°, and 10°C in 38-L black glass aquaria. Eggs and larvae were not incubated at 2°C because of the high mortality observed at this temperature in earlier studies (Laurence 1975, Buckley 1982). Embryos were gradually acclimated to the incubation temperatures at the rate of 1°C per 6 hours. After hatching, larvae were fed live zooplankton collected in the Narragansett Bay area and sieved to select the appropriate size fraction. Plankton densities were maintained at greater than 2 plankters per mL.

**Table 1**

Experimental design. Three *Pseudopleuronectes americanus* females were spawned at each of two acclimation temperatures (2°, 7°C). Subsamples of about 1500 eggs from each female were incubated in separate containers at each of three temperatures (4°, 7°, 10°C). Triplicate samples of 40 larvae each were taken from each tank for biochemical analysis.

| Stage | Temperature | Time |
|---|---|---|
| Adults | 3.5°C | Capture |
| | ↙ ↘ | |
| | Acclimation | |
| Adults–Gamets | 2°C 7°C | 48–51 days |
| | ↓ ↓ | |
| | Incubation | |
| Embryos–Larvae | 4,7,10°C 4,7,10°C | 13–29 days |

Groups of 10 larvae were examined daily, between 0800 and 1100 hours, under a dissecting microscope to establish the day of completion of yolksac absorption and first feeding. Larvae were judged to have completed yolksac absorption when 5 out of 10 larvae had no visible yolk. Larvae were judged to have initiated feeding when 5 out of 10 larvae examined had food visible in their gut. At hatching and first feeding 10 larvae from each group (one unique combination of acclimation and incubation temperatures for each female) were measured for standard length with a filar micrometer in a dissecting microscope. Yolk volume was estimated using the equation for a prolate spheroid:

$$V = (\pi/6)\, LH^2$$

where $L$ is the length and $H$ is the height of the yolksac (Laurence 1973). Triplicate groups of 40 larvae each were sampled at the same times for biochemical analysis. Larvae were homogenized in 2.0 mL of ice-cold distilled water using an all-glass tissue grinder. Subsamples of 1.4 and 0.1 mL of homogenate were used for analysis of nucleic acids and protein, respectively, as outlined in Buckley (1979). Nucleic acids were determined using a modification of the Schmidt-Thannhauser method. A modification of the Lowry method was used for determination of protein. Coefficients of varia-

**Table 2**
Size and number of injections for individual *Pseudopleuronectes americanus* females, and percent fertility and hatch of their offspring.

| Acclimation T (°C) | Tag number | Length (mm) | Weight (g) | No. injections | Fertility (%) | Incubation T (°C) | Hatch (%) | Age at hatch (d) | Age at first feeding (d) |
|---|---|---|---|---|---|---|---|---|---|
| 2 | 335 | 280 | 290 | 4 | 98 | 4 | 85 | 20 | 9 |
| | | | | | | 7 | 80 | 11 | 7 |
| | | | | | | 10 | 72 | 7 | 2 |
| 2 | 217 | 301 | 389 | 4 | 75 | 4 | 85 | 17 | 7 |
| | | | | | | 7 | 80 | 10 | 7 |
| | | | | | | 10 | 70 | 8 | 5 |
| 2 | 218 | 290 | 315 | 3 | 96 | 4 | 85 | 16 | 7 |
| | | | | | | 7 | 80 | 10 | 7 |
| | | | | | | 10 | 70 | 7 | 5 |
| 7 | 857 | 245 | 345 | 2 | 96 | 4 | 85 | 15 | 8 |
| | | | | | | 7 | 80 | 10 | 6 |
| | | | | | | 10 | 70 | 7 | 4 |
| 7 | 067 | 303 | 373 | 4 | 98 | 4 | 80 | 14 | 11 |
| | | | | | | 7 | 70 | 10 | 6 |
| | | | | | | 10 | 70 | 7 | 4 |
| 7 | 276 | 357 | 627 | 3 | 98 | 4 | 80 | 14 | 11 |
| | | | | | | 7 | 80 | 7 | 6 |
| | | | | | | 10 | 80 | 7 | 6 |

tion (sample standard deviation as a percent of the mean) for replicate analyses on portions of a fresh or frozen homogenate run within one week of preparation were 3% for RNA, 8% for DNA, and 5% for protein.

Data analysis was done using SAS System Software for personal computers (SAS 1985). The GLM procedure was used for analysis of variance because of the unbalanced design. Differences among main effect means were tested for significance using Tukey's studentized range test.

## Results

Between 48 and 51 days after capture, three females were spawned at each acclimation temperature after receiving between two and four hormone injections (Table 2). There was no significant difference in either the number of injections administered or the length of female parents between acclimation temperature groups (analysis of variance, $P \leq 0.05$). Spawning females ranged in length from 245 to 357 mm with a mean of 296 mm. Based on length-at-age data for winter flounder from the Niantic River, CT (Northeast Utilities 1987), this corresponds to a range in age of 3–6 years. Fertilization rate was high, ranging from 75 to 98% with a mean of 94%. Acclimation temperature or the number of hormone injections had no significant effect on the fertilization rate ($P \leq 0.05$). Percent hatch ranged from 70 to 85% with a mean of 78%. Hatch rates were significantly higher at the lower incubation temperatures but unaffected by acclimation temperature of the parents ($P \leq 0.05$).

At all combinations of acclimation (prespawning) and incubation (postspawning) temperature, completion of yolksac absorption occurred within one day of first feeding. Age at hatch and age at first feeding were inversely related to incubation temperature. Spawning temperature had an effect on age at hatch but not on age at first feeding. No interactive effect of adult acclimation temperature and embryo incubation temperature was observed on the rate of these developmental processes ($P \leq 0.05$).

The mean standard length and chemical content of larvae at hatching and first feeding are given in Tables 3 and 4. Standard length and DNA content generally increased over this period (Fig. 1). The decrease in protein content between hatching and first feeding indicates a net catabolism of protein during the period.

The effects of selected factors on the size and chemical content of larvae at hatching and at first feeding were evaluated using analysis of variance (Table 5). In SAS notation, the general form of the model used was:

$$Y = A\ B\ C(A)\ A*B$$

where $Y$ is the dependent variable and $A$, $B$, and $C$

**Table 3**

Length, yolksac volume, and chemical content of *Pseudopleuronectes americanus* larvae at hatching. Values are the estimated means along with the standard deviation. For standard length and yolksac volume, $N = 30$ (10 larvae from each of 3 females). For RNA, DNA, and protein content, $N = 9$ (3 pools of 40 larvae each from 3 females). Percents in brackets are coefficients of variation of the grand mean. Where the interaction between adult spawning temperature and embryo incubation temperature was not significant, main-effects means were calculated and Tukey's studentized range test applied to these values. Where the temperature interaction factor was significant, simple main effects were tested. Values in a row with a superscrip letter in common or bracketed values in a column are not significantly different ($P \leq 0.05$).

| Spawning temperature (°C) | Incubation temperature (°C) 4 | 7 | 10 | $\bar{x}$ |
|---|---|---|---|---|
| | | Standard length (mm) | | |
| 2 | [3.61 ± 0.15[a] | [3.45 ± 0.17[b] | 3.40 ± 0.14[b] | |
| 7 | [3.33 ± 0.16[a] | [3.46 ± 0.09[b] | — | |
| $\bar{x}$ | | | | 3.45 ± 0.18 (6.1%) |
| | | Yolksac volume ($mm^3$) | | |
| 2 | 0.08 ± 0.04 | 0.05 ± 0.02 | 0.05 ± 0.02 | 0.06[a] |
| 7 | 0.08 ± 0.04 | 0.05 ± 0.01 | — | 0.07[a] |
| $\bar{x}$ | 0.08[a] | 0.05[b] | 0.05[b] | 0.06 ± 0.03 (50%) |
| | | RNA content (μg/larva) | | |
| 2 | 1.32 ± 0.16 | 1.18 ± 0.20 | 1.17 ± 0.09 | 1.22[a] |
| 7 | 1.27 ± 0.13 | 1.13 ± 0.08 | 1.05 ± 0.08 | 1.16[b] |
| $\bar{x}$ | 1.30[a] | 1.16[b] | 1.11[b] | 1.19 ± 0.16 (13.1%) |
| | | DNA content (μg/larva) | | |
| 2 | [0.34 ± 0.06[a] | [0.2820.04[b] | [0.36 ± 0.04[a] | |
| 7 | [0.33 ± 0.05[b] | [0.39 ± 0.04[a] | [0.33 ± 0.03[b] | |
| $\bar{x}$ | | | | 0.34 ± 0.06 (16.7%) |
| | | Protein content (μg/larva) | | |
| 2 | 17.3 ± 2.4 | 15.7 ± 4.2 | 15.8 ± 2.7 | 16.2[a] |
| 7 | 15.2 ± 2.2 | — | 15.6 ± 1.7 | 15.3[a] |
| $\bar{x}$ | 16.1[a] | 15.7[a] | 15.7[a] | 15.9 ± 2.8 (17.5%) |

**Table 4**

Length and chemical content of *Pseudopleuronectes americanus* larvae at first feeding. Values and statistics are as given for Table 3.

| Spawning temperature (°C) | Incubation temperature (°C) 4 | 7 | 10 | $\bar{x}$ |
|---|---|---|---|---|
| | | Standard length (mm) | | |
| 2 | [4.40 ± 0.15[a] | [4.18 ± 0.30[b] | [3.96 ± 0.15[c] | 4.21[a] |
| 7 | [4.35 ± 0.09[a] | [4.14 ± 0.19[b] | [4.05 ± 0.14[b] | 4.19[a] |
| $\bar{x}$ | | | | 4.20 ± 0.25 (5.9%) |
| | | RNA content (μg/larva) | | |
| 2 | [1.30 ± 0.13[a] | [1.21 ± 0.15[a] | [0.89 ± 0.01[b] | |
| 7 | [1.17 ± 0.12[a] | [1.01 ± 0.08[b] | [1.21 ± 0.15[a] | |
| $\bar{x}$ | | | | 1.15 ± 0.18 (15.2%) |
| | | DNA content (μg/larva) | | |
| 2 | 0.41 ± 0.06 | 0.35 ± 0.07 | 0.38 ± 0.02 | 0.38[a] |
| 7 | 0.37 ± 0.03 | 0.43 ± 0.06 | 0.38 ± 0.05 | 0.39[a] |
| $\bar{x}$ | 0.39[a] | 0.39[a] | 0.38[a] | 0.39 ± 0.05 (13.7%) |
| | | Protein content (μg/larva) | | |
| 2 | [13.3 ± 1.6[a] | [12.0 ± 1.8[a,b] | [11.0 ± 2.0[b] | |
| 7 | [13.1 ± 1.0[a] | [13.4 ± 0.9[a] | [11.1 ± 1.2[b] | |
| $\bar{x}$ | | | | 12.8 ± 1.6 (12.5%) |

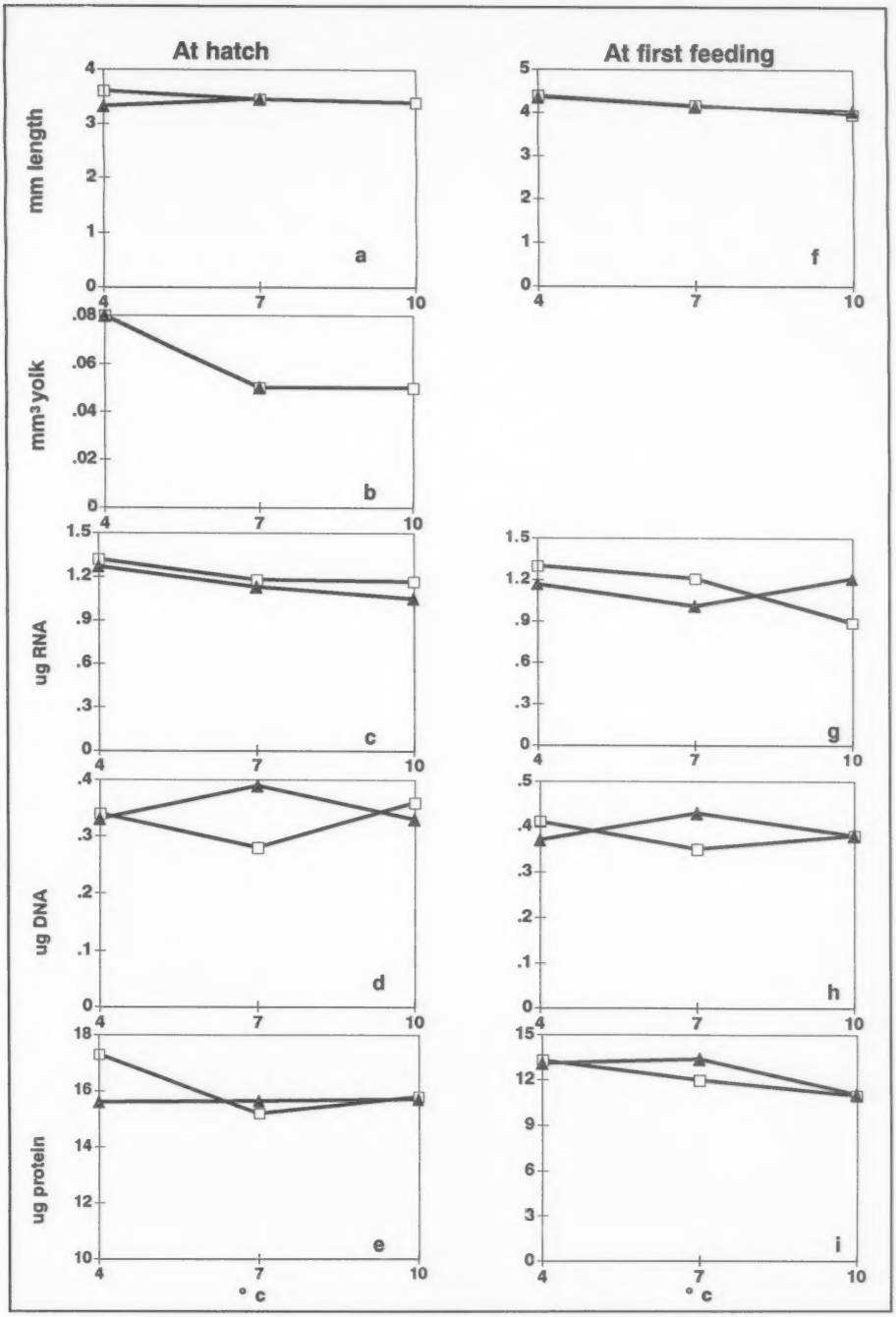


**Figure 1**

Standard length, yolk volume, and biochemical composition of *Pseudopleuronectes americanus* larvae at hatching and first feeding. □ Tsp = 2°C; ▲ Tsp = 7°C.

**Table 5**

Analysis of variance for factors affecting size and chemical content of *Pseudopleuronectes americanus* larvae at hatch and first feeding. Tsp = adult acclimation and spawning temperature; Tinc = embryo and larval incubation temperature; T × T = temperature interaction; Block = female tag number. $*P \leq 0.05$, $**P \leq 0.01$, $***P \leq 0.001$. Where the temperature interaction is significant, $F$ values for Tsp and Tinc are not given.

| | | Tsp | Tinc | T × T | Block | Total |
|---|---|---|---|---|---|---|
| | | | **At Hatch** | | | |
| Larval length (mm) | df | 1 | 2 | 2 | 4 | 139 |
| | $F$ value | | | 25.17*** | 13.66*** | |
| Yolk volume ($mm^3$) | df | 1 | 2 | 2 | 4 | 139 |
| | $F$ value | 0.00 | 12.26*** | 0.05 | 2.40* | |
| RNA (μg/mg) | df | 1 | 2 | 2 | 4 | 49 |
| | $F$ value | 4.68* | 15.94*** | 0.18 | 10.16*** | |
| DNA (μg/mg) | df | 1 | 2 | 2 | 4 | 49 |
| | $F$ value | | | 24.15*** | 8.41*** | |
| Protein (μg/mg) | df | 1 | 2 | 1 | 4 | 36 |
| | $F$ value | 0.00 | 1.11 | 0.01 | 15.59*** | |
| | | | **At First Feeding** | | | |
| Larval length (mm) | df | 1 | 2 | 2 | 2 | 169 |
| | $F$ value | | | 5.07** | 8.08*** | |
| RNA (μg/mg) | df | 1 | 2 | 2 | 4 | 41 |
| | $F$ value | | | 40.78*** | 12.29*** | |
| DNA (μg/mg) | df | 1 | 2 | 2 | 4 | 39 |
| | $F$ value | 0.27 | 1.38 | 3.13 | 1.90 | |
| Protein (μg/mg) | df | 1 | 2 | 2 | 4 | 34 |
| | $F$ value | | | 6.32** | 11.93*** | |

are independent class variables (SAS Institute 1985). $A$ is the acclimation and spawning temperature (Tsp); $B$ is the embryo and larval incubation temperature (Tinc); $C$ is the block effect or individual female tag number (Block). This maternal factor is nested within the acclimation temperature and represents the variability among individual spawning females. This factor was added to the model to block out fish-to-fish variability. It was significant for all dependent variables tested (Table 5). $A*B$ is the interaction of acclimation and incubation temperatures.

Significant interactions between spawning and incubation temperature were observed at hatch for length and DNA content, and at first feeding for length, RNA, and protein content. In these cases, where the effects of spawning temperature and incubation temperature were nonadditive, simple main effects were tested at each spawning and incubation temperature using Tukey's studentized range test. Where no temperature interaction was observed (yolk volume, RNA, and protein content at hatch, and DNA content at first feeding) main-effects means were calculated and differences among main-effects means were tested for significance using Tukey's studentized range test.

At hatching, standard length showed a significant temperature interaction (Table 5). At a spawning temperature of 2°C, standard length decreased with increasing incubation temperature (Table 3). At a spawning temperature of 7°C, standard length was higher at an incubation temperature of 7°C than at 4°C. Yolk volume showed no significant temperature interaction, was unaffected by spawning temperature, and was highest at the lowest incubation temperature of 4°C. RNA content at hatch showed no significant temperature interaction and decreased with both increasing spawning and incubation temperature. DNA content at hatch showed a significant temperature interaction. At a spawning temperature of 2°C, DNA content was lowest at the intermediate incubation temperature (7°C). At a spawning temperature of 7°C, DNA content was highest at this intermediate incubation temperature. Protein content at hatch showed no temperature interaction and was unaffected by either spawning or incubation temperature.

At first feeding, standard length showed a significant temperature interaction. At both spawning temperatures (2° and 7°C) standard length decreased with increasing incubation temperature (Table 4). RNA content at first feeding showed a significant temperature interaction. At a spawning temperature of 2°C, RNA content was lowest at the highest incubation temperature (10°C). At a spawning temperature of 7°C, RNA

content was lowest at the intermediate incubation temperature (7°C). DNA content at first feeding showed no significant temperature interaction and was unaffected by either spawning or incubation temperature. Protein content at first feeding showed a significant temperature interaction. At both spawning temperatures, protein content decreased with increasing incubation temperature.

## Discussion

Winter flounder spawn and embryos survive over a wide range of temperatures. In the laboratory, Williams (1975) observed survival of embryos between −1.8° and 15°C. Rogers (1976) reported survival between 3° and 14°C. While 2°C is close to the temperature of maximum egg production, winter flounder larvae require water temperatures above 2°C for survival to metamorphosis (Laurence 1975, Buckley et al. 1982). Spawned through the late winter and early spring, winter flounder embryos and larvae generally experience gradually increasing water temperatures. In shallow estuaries and bays, however, embryos and larvae may be subjected to large fluctuations in salinity and water temperature over relatively short periods of time, or to prolonged periods of abnormal warming or cooling. The effects of such changes in water temperature on survival and growth of the early-life stages of winter flounder are largely unknown.

Inverse relations between water temperature (during late winter and early spring) and indices of recruitment have been reported for winter flounder (Jeffries and Johnson 1974, Jeffries and Terceiro 1985, Northeast Utilities 1988). The shape of larval abundance curves, a parameter affected by water temperature, has also been related to recruitment; cold years with broad shallow abundance curves produce good year-classes (Northeast Utilities 1988).

The size and chemical composition of larvae at initiation of feeding provide useful criteria for evaluation of these temperature effects, and may provide insight into causal mechanisms. Feeding initiation is the end point of the period of reliance on endogenous energy reserves that commences at ovulation. Increased larval size confers increased potential for survival, since larger larvae are better able to avoid size-dependent predation, capture food, and survive periods of starvation (Blaxter and Hempel 1966, Rosenberg and Haugen 1982, Bailey and Battey 1984, Knutsen and Tilseth 1985). DNA content is an index of cell number and RNA content an index of the capacity for protein synthesis and hence growth (Bulow 1987). Buckley et al. (In prep.) demonstrated direct relations between size and RNA content of yolksac winter flounder larvae and survival for the first month of life in the laboratory. Size of larvae at first feeding is dependent upon egg size at spawning and the efficiency of production of larval tissue (yolk-conversion efficiency).

Based on observations of the timing of yolk absorbtion and first feeding, and the size and composition of winter larvae produced by a single female spawned at 2°C, Buckley (1982) speculated that eggs spawned at low temperatures (2°) may be poorly suited for growth and survival at high temperatures (10°C) within the range of tolerance of winter flounder. The present factorial study of six females spawned at low (2°C) and high (7°C) temperatures confirmed and extended these earlier findings. However, unlike the earlier study, first feeding occurred within one day of completion of yolk absorbtion at all combinations of adult acclimation (prespawning) and incubation temperature (Table 2). The present study, with the spawn from six winter flounders, demonstrated the importance of variability at the level of individual females in determining size and composition of winter flounder larvae (Tables 3 and 4). Adult acclimation (prespawning) temperature was important alone or in combination with embryo incubation temperature in determining length and RNA and DNA content at hatch, and in determining length and RNA and protein content at first feeding (Table 5). Embryo incubation temperature was important alone or in combination with adult acclimation temperature in determining larval size, yolksac volume, RNA and DNA content at hatch, and in determining length and RNA and protein content at first feeding. At first feeding, size and chemical content of eggs spawned by adults acclimated to 2°C were maximized at the lowest incubation temperature (4°C). Eggs spawned at 7°C produced the longest first-feeding larvae at 4°C, while DNA and protein content were highest at the intermediate incubation temperature (7°C) and RNA content was highest at the warmest incubation temperature (10°C). The largest larvae, whether measured by length or chemical content, were produced at the lowest combination of acclimation and rearing temperatures. RNA content, which is critical to protein synthesis and growth, was highest at first feeding in larvae incubated at 4°C for eggs produced at 2°C, and at 10°C for eggs produced at 7°C. RNA content was lowest in first-feeding larvae produced from eggs spawned at 2°C and incubated at 10°C. This group represented the largest difference between spawning and incubation temperature.

Hempel and Blaxter (1967) reported differences in fecundity and egg size between Atlantic herring stocks spawning at different temperatures. Stocks spawning at colder temperatures produced fewer but larger eggs. Tanasichuk and Ware (1987) working with Pacific herring found that both size-specific fecundity and egg

size, but not size-specific ovary weight, were related to seawater temperature 60–90 days before spawning. Again, fecundity increased with increasing temperature while egg size decreased.

Results from this study demonstrate that water temperatures during the latter stages of gamete maturation (48–51 days prior to spawning) and during embryo and larval development affect the size and composition of winter flounder larvae produced. Further, the interaction between acclimation temperature of adults and incubation temperature of embryos and larvae also appears to have a strong effect on size and composition of larvae. While the number of oocytes entering vitellogenesis is probably determined earlier in the reproductive cycle (Brown 1957, Dunn 1970, Tyler and Dunn 1976, Burton and Idler 1984), several important functions occur during the latter stages of gamete development, including further deposition of yolk and final meiotic division.

Our data on size and chemical composition of winter flounder at hatching and first feeding suggest a more complex relation between water temperature and larval size than observed between water temperature and egg size. These data may help explain some of the variability observed in the relation between yolk-conversion efficiency or maximum larval size and incubation temperature (Sweet and Kinne 1964, Alderdice and Forrester 1968, Laurence and Rogers 1976, Linden et al. 1980, Johns et al. 1981, Laurence and Howell 1981, Buckley 1982). Our data suggest that larval size and composition at hatch and first feeding are dependent not only upon incubation temperature but also upon water temperature during the final stages of gamete maturation and upon the interaction of water temperature during these two time-periods. This implies that the contents of the egg are modified in some way in response to water temperature prior to spawning. Most likely, this temperature response goes beyond simply producing a larger or smaller egg with components in the same proportion. The ratio of major organic components including protein, lipids, carbohydrates, and nucleic acids may be altered in response to temperature. More subtle, but possibly more significant, changes in the composition of the developing oocyte in response to water temperature may include alterations in the content, composition, activity, or stability of enzymes, hormones, maternal messenger RNA, and stable RNA (tRNA and rRNA). Any conclusions about the efficiency of yolk utilization at different incubation temperatures should take into account the thermal history of the spawning adults.

Winter flounder reproductive strategy has most likely evolved to exploit the dramatic increase in water temperature during the spring in the shallow estuaries along the northwest margin of the Atlantic Ocean. Between spawning and metamorphosis, a period of about 2 months in winter flounder, water temperatures warm an average 10°C (from ~2° to 12°C) affecting not only the abundance and composition of predators and prey but also the rates of metabolic processes (Laurence 1975, 1977). This maximizes size and condition of first-feeding larvae at low temperatures (Table 4), allows relatively long resistance to starvation at intermediate temperatures, and facilitates rapid larval and postlarval growth at higher temperatures (Buckley 1982). Mortality of late embryos and larvae at cold temperatures (≤2°C) (Laurence 1975, Buckley 1982) indicates that good survival of winter flounder is dependent upon the expected spring warming. While gametogenesis and embryo and larval development show a wide range of temperature tolerance in winter flounder, these processes appear to have been optimized for cold winter temperatures followed by gradual spring warming. Our data suggest that cold winters followed by gradual spring warming favor good survival and recruitment of winter flounder by facilitating production of the largest larvae at first feeding (high standard length and DNA content) in the best condition (high RNA and protein content). These data may explain in part the observed correlation between cold years and strong year-classes (Jeffries and Johnson 1977, Jeffries and Terceiro 1985, Northeast Utilities 1988).

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**Abstract.**—This study represents an attempt to distinguish between normal seasonal variations and pollutant-related changes in the blood chemistry of the windowpane flounder *Scophthalmus aquosus*. Three stations in Long Island Sound, USA, were chosen to provide a pollutant gradient. Windowpane flounder were collected from the three stations monthly, when possible, over a period of three years. Seasonal variations were noted in hematocrit, plasma osmolality, sodium, potassium, and calcium. Station-related differences were demonstrated in osmolality, hematocrit, and hemoglobin. The same species was subjected to 60-day laboratory exposures to mercury, cadmium, or copper. Neither copper nor cadmium produced a significant difference in any variable measured. Following exposure to mercury, there were significant differences between controls and exposed animals in plasma sodium and calcium.

# Blood Chemistry of the Windowpane Flounder *Scophthalmus aquosus* in Long Island Sound: Geographical, Seasonal, and Experimental Variations

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The geographical situation of Long Island Sound presents unique questions on the distribution of anthropogenic pollutants and the effects of such pollutants on the resident animal population. The western end of the Sound is heavily populated and industrialized. Much of the bottom in the western portions of the Sound consists of fine-grained sediments, with a potential for adsorbing and retaining contaminants (Hunt 1979, Reid et al. 1979). Tidal flushing is limited in the far western end of the Sound; it has been reported that exchange with the East River adds 15 $m^3$/second of effluent to western Long Island Sound (Bowman 1976).

In contrast, the more eastern portions of the Sound are open to considerable tidal flushing and are bordered by less populated and less industrialized areas. There is a decrease in fine-grained sediments from west to east with a concomitant decrease in the capacity of the sediment to retain contaminants (Hunt 1979, Reid et al. 1979). The physical and geographical differences are reflected in an increase from east to west in sediment levels of heavy metals (Greig et al. 1977, Hunt 1979, NOAA 1988), PCBs (Chytalo 1979, NOAA 1988), and PAHs (NOAA 1988).

The present study is an attempt to assess the effects on a local species of the contaminant levels found in Long Island Sound. Stations were selected on the basis of providing a pollutant gradient and of being located within an area that could be sampled on a day-trip basis, thereby expediting monthly sampling (Fig. 1). Station 1 was off Roanoke Point, New York (lat. 40°58′50″N, long. 72°45′00″W), near the eastern end of the central basin. Reid et al. (1979) reported that this station had less than 5% fine-grained sediments. Greig et al. (1977) reported a sediment cadmium concentration of 1.1 mg/kg dry weight, a copper concentration of 4.0 mg/kg, and a lead concentration of <6.0 mg/kg. Station 2 was off Milford, Connecticut (lat. 40°09′01″N, long. 73°00′00″W), near the western end of the central basin. Reid et al. (1979) reported that this station had a fine-grained sediment level between 5 and 50%. Greig et al. (1977) reported sediment cadmium and mercury levels below detectable limits, a copper concentration of 43.3 mg/kg, and a lead concentration of 19.0 mg/kg. Station 3, Hempstead Harbor, New York (lat. 40°53′50″N, long. 73°49′90″W) is in the western end of Long Island Sound. Reid et al. (1979) reported a fine-grained sediment content of >50%. Greig et al. (1977) reported a cadmium concentration of 1.4 mg/kg, a copper concentration of 175.0 mg/kg, a mercury concentration of 0.7 mg/kg, and a lead concentration of 110.0 mg/kg in the sediment. NOAA (1988) reported a total PCB concentration of 255.5 μg/kg and a total PAH concen-

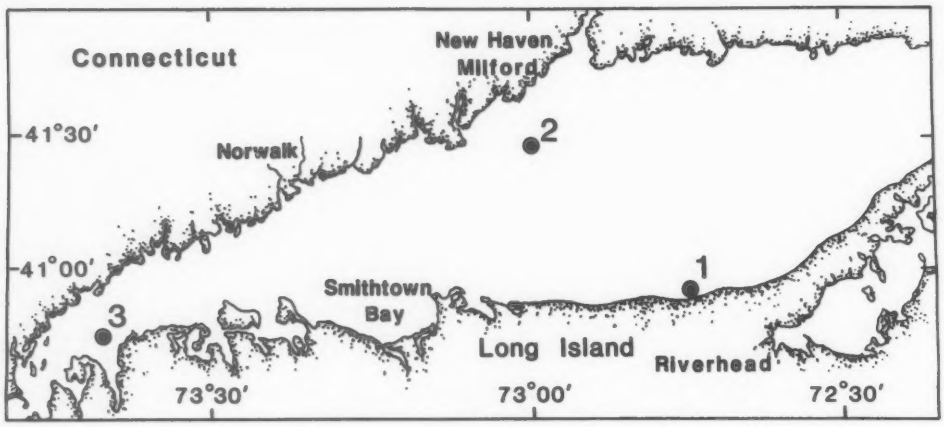


**Figure 1**

Long Island Sound stations sampled for *Scophthalmus aquosus*: Station 1, off Shoreham, NY, 5.5 m; Station 2, off Milford, CT, 15.2 m; Station 3, Hempstead Harbor, NY, 10.7 m.

tration of 5366 μg/kg in the sediments of Hempstead Harbor.

The windowpane flounder *Scophthalmus aquosus* was chosen as a test animal because it is one of the few species available in the Long Island Sound area throughout the year. The possibility of some movement between stations is a consideration in this type of study. However, Moore (1947) reported on the basis of tagging studies that, although individuals have been shown to move over large distances, no seasonal migration of windowpane flounder is indicated and that this species is relatively stationary.

This study utilized blood chemistry as an indication of stress in the fish. Several investigators have suggested that the study of blood may ultimately be as useful in assessing the health of fish as it is in diagnosing human health (Blaxhall and Daisley 1973, Hickey 1976). Fish blood chemistry has not received the same critical study as has human (Wedemeyer and Yasutake 1977). A given species of fish in its normal habitat is likely to be subjected to a wide range of natural conditions, any of which may be reflected in its blood chemistry. Johansson-Sjöbeck et al. (1975) noted that hematocrit increased and hemoglobin decreased in eels subjected to starvation, both returning to control levels within 164 days. DeWilde and Houston (1967) reported an increase in hematocrit and hemoglobin with an increase in acclimation temperature in rainbow trout; the degree of response depended on season. Effects of heavy-metal exposure on fish blood have been demonstrated (Christensen et al. 1972; Calabrese et al. 1975; Dawson 1979, 1982). Within the same species, freshwater-adapted fish often exhibit blood chemistry which is different from that of fish adapted to seawater (Courtois 1976). Snieszko (1960) emphasized the need to consider two sets of standards in using hemotological methods in hatcheries: one general standard for the species, and a second standard that determines a normal value for the parameter at a particular hatchery.

Although the objective of the present study was to obtain information on pollutant-related stress, it was necessary to consider seasonal changes as well in order to distinguish between the effects of pollutants and those that represent a normal response to changing natural conditions. Although seasonal changes in fish blood have received little attention in the literature, such changes have been documented in the winter flounder (Bridges et al. 1976), the striped bass (Lochmiller et al. 1989) and the rainbow trout (DeWilde and Houston 1967). In addition, the values for hematological measurements vary from species to species, but few species have received sufficient study to allow a realistic estimate of their normal ranges under a reasonable variety of conditions.

The field study described here was supplemented by a series of three laboratory exposures of the same species to heavy metals. Although laboratory exposures are subject to criticism on the grounds that they do not correspond closely to natural conditions, they do make it possible to attribute changes to a particular pollutant, which is not often possible in the field.

## Materials and methods

### Field study

Windowpane flounder for the field study were collected by otter trawl using 30-minute tows at the three desig-

nated stations and held in running seawater aboard the boat until blood samples were taken, generally within 1 hour after the fish were collected. On occasion, because of inclement weather, it was necessary to return to the laboratory and sample the fish at dockside; in that case, the interval between capture and sampling was up to 4 hours.

The stations were sampled monthly unless inclement weather or boat repairs precluded sampling. Generally, blood samples were taken from 20 fish at each station; if fewer fish were obtained, sample numbers were necessarily smaller. Of 102 collections used, 67 consisted of 20 fish each, 33 of 10–19 fish, and one each of 8 and 9 fish. Respective lengths of fish sampled at Station 1, 2, and 3 were $26.7 \pm 0.13$, $25.0 \pm 0.16$, and $25.6 \pm 0.15$ cm. Hematocrit (Hct), hemoglobin (Hb), plasma osmolality, sodium, potassium, and calcium were measured on each blood sample. Prior to each fish collection, a bottom-water sample was collected for measurement of temperature, salinity, and dissolved oxygen. Four preliminary collections were made at each station in 1979; intensive sampling continued from May 1980 through April 1983.

## Exposure studies

Windowpane flounder were exposed to mercury, copper, or cadmium in the laboratory. Fish used in the exposure studies were collected by otter trawl using 15- or 30-minute tows in the vicinity of Milford, Connecticut, and transported to the laboratory in running seawater. They were held at the laboratory for at least 2 weeks prior to exposure. In general, exposures were conducted during the colder months when the fish do not normally feed much. However, they were given small amounts of minced surf clam *Spisula solidissima* weekly. The fish measured $24.8 \pm 0.21$ cm in length and $158.4 \pm 4.2$ g in weight.

Three 60-day exposures were performed: the first used $HgCl_2$ at a nominal mercury concentration of 5 or 10 μg/L, the second used $CuCl_2 \cdot 2H_2O$ at a nominal copper concentration of 10 or 20 μg/L, and the third used $CdCl_2 \cdot 2½H_2O$ at a nominal cadmium concentration of 5 or 10 μg/L. Measured concentrations were $5.1 \pm 0.60$ ppb and $12.7 \pm 2.20$ ppb for low and high cadmium concentrations, and $19.2 \pm 1.4$ for the high copper concentration. Background metal levels were below 1 μg/L for mercury, below 5 μg/L for copper, and below 1 μg/L for cadmium. The fish were exposed in 285-L fiberglass tanks filled to 225 L with sand-filtered Milford Harbor seawater by a proportional dilution apparatus (Mount and Brungs 1967). The diluter controlled the intermittent delivery of toxicant-containing or control seawater at a flowrate of 1.5 L every 2.5 minutes throughout the exposure period. This provided a flow of 864 L per day and an estimated 90% replacement time of 15 hours (Sprague 1969). The seawater was at ambient salinity during the exposures. The temperature was slightly above ambient because the water was held in the heated building during filtration and delivery.

Duration of the mercury exposure was 22 December 1979–20 February 1980. The salinity range during that time was 25.0–26.9‰. Temperature in the exposure tanks was 8°C at the beginning of the exposure, dropping to 3-4°C throughout most of the month of February when the exposure was completed. During the mercury exposure, each tank held 5 fish for a total of 20 fish per concentration and 20 controls.

The copper exposure ran from 7 January through 8 March 1983. Salinity during the exposure period was 24.4–26.4‰. Temperature was 9°C at the beginning of exposure, dropped to a low point of 6°C in mid-February, and gradually rose to 9°C at the end. Three tanks at each concentration held 4 fish per tank.

Duration of the cadmium exposure was 27 January–28 March 1984. Salinity range during that time was 22.6–25.9‰. Temperature was 6.5°C at the beginning of the exposure, rising to 8.5°C at the end. The lowest temperature recorded was 5.0°C on 3 February. Twenty fish were exposed per concentration, 5 fish per tank.

## Blood chemistry

The parameters measured were hematocrit (Hct), hemoglobin (Hb), mean corpuscular hemoglobin concentration (MCHC), plasma osmolality, sodium, potassium, and calcium. Erythrocyte counts (RBC) and calculations of mean corpuscular hemoglobin (MCH) and mean corpuscular volume (MCV) were performed only on animals used in exposures.

Blood was collected from each animal by cardiac puncture using a 3-mL plastic syringe and a 20- or 22-gauge needle. The sample was transferred gently into an 8-mL glass vial containing 150 units of dried ammonium heparinate as an anticoagulant. Immediately following collection of the last blood sample, a portion of each blood sample was centrifuged at 12 000 g and the plasma frozen for later determination of osmolality, sodium, potassium, and calcium. The remaining whole-blood sample was used for the determination of hemoglobin, hematocrit, and erythrocyte counts. Hemoglobin was determined by the cyanmethemoglobin method using Hycel chemicals. Microhematocrits were determined following centrifugation for 5 minutes at 13 500 g. Erythrocyte counts were made in a hemacytometer; blood samples were diluted 1:200 with Yokoyoma's solution (Katz 1950). Plasma osmolality was determined with an

**Table 1**

Effects of 60-day exposure to mercury on blood of windowpane flounder *Scophthalmus aquosus* in Long Island Sound. Values are mean ± standard error, with number of samples in parentheses. Number of samples is often fewer than that of fish exposed because of clotting or pooling of samples.

| Test | Control | Mercury concentration 5 μg/L | 10 μg/L |
|---|---|---|---|
| Hematocrit (%) | 22.00 ± 1.3 (17) | 25.00 ± 1.4 (15) | 24.00 ± 1.6 (18) |
| Hemoglobin (g/100 mL) | 4.10 ± 0.2 (17) | 4.30 ± 0.3 (15) | 3.40 ± 0.2 (18) |
| Erythrocytes ($10^6$ cells/mm$^3$) | 2.14 ± 0.17 (9) | 2.13 ± 0.14 (9) | 2.41 ± 0.29 (10) |
| MCV ($\mu^3$/cell) | 96.60 ± 5.7 (9) | 109.80 ± 4.0 (9) | 103.90 ± 9.1 (10) |
| MCH (pg/cell) | 20.20 ± 1.6 (9) | 21.10 ± 1.2 (9) | 18.90 ± 1.2 (10) |
| MCHC (g/100 mL) | 19.10 ± 1.0 (17) | 18.40 ± 0.6 (15) | 18.10 ± 0.5 (18) |
| Na (mEq/L) | 179.00 ± 3.9 (11) | 181.00 ± 3.5 (14) | *199.00 ± 3.3 (13) |
| K (mEq/L) | 8.21 ± 0.85 (11) | 6.93 ± 0.66 (14) | 8.52 ± 0.81 (13) |
| Ca (mEq/L) | 4.95 ± 0.23 (11) | *3.91 ± 0.18 (14) | *3.60 ± 0.19 (13) |
| Osmolality (mOsm) | 338.00 ± 7.7 (9) | 328.00 ± 4.0 (14) | 331.00 ± 2.9 (12) |

MCV = Mean corpuscular volume
MCH = Mean corpuscular hemoglobin
MCHC = Mean corpuscular hemoglobin concentration
*Significantly different from controls ($P<0.05$).

Advanced 3L osmometer; the effect of the added heparin on osmolality was negligible. Plasma sodium, potassium, and calcium concentrations were measured with a Coleman 51 flame photometer. At times it was necessary to pool the small plasma samples, resulting in slightly fewer samples for plasma ions and osmolality. Mean corpuscular volume (MCV), mean corpuscular hemoglobin (MCH), and mean corpuscular hemoglobin concentration (MCHC) were determined using the following equations (Platt 1969):

MCV in $\mu^3$/cell = 10 Hct/RBC
MCH in pg/cell = 10 Hb/RBC
MCHC in g/00 mL packed red cells = 100 Hb/Hct

Statistical differences were determined by one-way analysis of variance and the Scheffe test (Hicks 1973).

## Results

### Exposure studies

Results of the 60-day exposure of windowpane flounder to mercury are summarized in Table 1. Red blood cells in the species appear to be unaffected by mercury at the test concentrations used in this study. Control flounder had a mean hematocrit of 22 ± 1.3%, a mean hemoglobin of 4.1 ± 0.2 g/100 mL, and a red cell count of 2.4 ± 0.17 × $10^6$ cells/mm$^3$. Following a 60-day exposure of the fish to 5 or 10 μg/L mercury, none of these variables differed signficantly from control values, nor did the indices calculated from the three variables (namely, MCH, MCV, and MCHC). The mean plasma sodium level in flounders exposed to 10 μg/L mercury was 199 ± 3.3 mEq/L, significantly higher than the control value of 179 ± 3.9 mEq/L. Plasma calcium decreased from the control value of 4.95 mEq/L to 3.91 ± 0.18 and 3.60 ± 0.19 m/Eq/L in animals exposed to 5 and 10 μg/L mercury, respectively. There were no significant differences between controls and mercury-exposed flounder in plasma potassium or osmolality (Table 1).

No significant difference was demonstrated between controls and animals exposed to either concentration of cadmium or copper in any of the parameters measured.

### Field study

The data from each season were divided by sex and compared using the Scheffe test; no significant sex-related differences were noted. The data were grouped into four size-classes (<20.0 cm, 20.1–25 cm, 25.1–30.0 cm, >30 cm) and compared for each season; no significant size-related differences were noted during any season. Because of the lack of differences, data from both sexes and all size-classes are shown together.

Overall, windowpane flounder taken from Station 3 had significantly higher hematocrits and hemoglobin concentrations than did those taken from Station 1.

Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

**Table 2**

Hematocrits of windowpane flounder *Scophthalmus aquosus* in Long Island Sound. Values are percent ± standard error, with number of fish in parentheses.

| Station | Winter | Spring | Summer | Fall |
|---|---|---|---|---|
| 1 | [a,b]20.6 ± 0.9 (78) | [c]23.2 ± 0.3 (172) | [d]24.9 ± 0.4 (140) | 23.8 ± 0.4 (139) |
| 2 | [b]22.1 ± 0.4 (105) | 24.0 ± 0.3 (182) | 24.6 ± 0.5 (132) | 23.9 ± 0.5 (137) |
| 3 | [b]23.2 ± 0.6 (93) | [a,c]26.6 ± 0.4 (178) | [d]25.4 ± 0.4 (136) | [a]25.9 ± 0.4 (139) |

[a]Significantly different ($P<0.05$) from all other stations in a given season.
[b]Significantly different from all other seasons at a given station.
[c,d]Significantly different pairs of seasons at a given station.

**Table 3**

Hemoglobin concentrations of windowpane flounder *Scophthalmus aquosus* in Long Island Sound. Units are g/100 mL ± standard error, with number of fish sampled in parentheses. No significant seasonal variations were demonstrated. Values from Station 1 are significantly lower than those from Stations 2 and 3; however, no contrasts between stations were significant when the data were separated by season.

| Station | Winter | Spring | Summer | Fall |
|---|---|---|---|---|
| 1 | 3.5 ± 0.13 (89) | 3.6 ± 0.11 (173) | 4.2 ± 0.11 (164) | 3.6 ± 0.12 (133) |
| 2 | 4.0 ± 0.13 (113) | 4.0 ± 0.11 (188) | 4.0 ± 0.12 (145) | 3.8 ± 0.11 (149) |
| 3 | 3.8 ± 0.14 (84) | 3.9 ± 0.10 (169) | 4.1 ± 0.10 (153) | 4.2 ± 0.14 (150) |

**Table 4**

Seasonal variations in blood chemistry of windowpane flounder *Scophthalmus aquosus* in Long Island Sound. Values are mean ± standard error. Because of the lack of significant differences between stations in these variables, data from all stations are combined.

| Variable | Winter | Spring | Summer | Fall |
|---|---|---|---|---|
| MCHC (g/100 mL) | 17.00 ± 0.04 (256) | 15.60 ± 0.03 (508) | 15.30 ± 0.04 (408) | 14.40 ± 0.04 (419) |
| Sodium (mEq/L) | [a]186.00 ± 0.4 (285) | 170.00 ± 0.3 (515) | [b]157.00 ± 0.3 (409) | [b]157.00 ± 0.3 (405) |
| Potassium (mEq/L) | [a]4.10 ± 0.18 (285) | [b]5.16 ± 0.14 (515) | [b,c]5.48 ± 0.15 (409) | [d]4.25 ± 0.16 (405) |
| Calcium (mEq/L) | 4.22 ± 0.12 (285) | [a]4.43 ± 0.10 (515) | 3.79 ± 0.10 (409) | [b]3.49 ± 0.11 (405) |

MCHC = Mean corpuscular hemoglobin concentration.
[a,b]Significantly different pairs.
[c,d]Significantly different pairs.

When the data from each station were separated by season, the difference between Stations 1 and 3 in hematocrit was significant during the winter, spring, and fall (Table 2). When the data on hemoglobin levels were separated by season, the difference between stations for any particular season was not significant (Table 3). Variations in hemoglobin from season to season were not significant (Table 3). At each station, the hematocrits of flounders collected during the winter were significantly lower than those of fish collected at any other season (Table 2).

Seasonal means in MCHC ranged from 14.4 to 17.0. There were no significant differences either between stations or between seasons (Table 4).

Plasma sodium levels varied by season but not by station. Because of the lack of difference between stations, the data from the three stations were treated together. The mean sodium value for winter-collected animals at all stations was 186 ± 0.4 mEq/L; this is significantly higher than the summer and fall values, both of which were 157 ± 0.3 mEq/L (Table 4).

Plasma potassium levels varied significantly by season but not by station. The highest levels were found in the summer. The mean value for summer-collected animals of 5.48 ± 0.15 mEq/L was significantly higher than either the winter value of 4.10 ± 0.18 mEq/L or the fall value of 4.25 ± 0.16 mEq/L (Table 4).

**Table 5**

Plasma osmolalities of windowpane flounder *Scophthalmus aquosus* in Long Island Sound. Units are mOsm ± standard error, with number of fish in parentheses. Within each station, groups which are not significantly different are underlined.

| Station | Winter | Spring | Summer | Fall |
|---|---|---|---|---|
| 1 | *392 ± 5 (89) | *387 ± 2 (167) | 390 ± 2 (129) | *401 ± 2 (124) |
| 2 | 377 ± 2 (109) | 377 ± 2 (170) | 393 ± 3 (113) | *389 ± 3 (118) |
| 3 | 380 ± 2 (87) | 374 ± 2 (176) | *383 ± 2 (134) | *377 ± 2 (132) |

*Significantly different ($P<0.05$) from all other stations at a given season.

There were no significant differences between stations in plasma calcium levels. The only seasonal variation was a significant difference between the spring value of 4.43 ± 0.10 mEq/L and the fall value of 3.49 ± 0.11 mEq/L (Table 4).

Overall, plasma osmolalities of fish collected from Station 3 were significantly lower than those of fish collected from Station 1. When the data were separated by season, the difference between Stations 1 and 3 for each season was significant (Table 5). During the winter, spring, and fall, plasma osmolalities from Station 2 were also significantly lower than those from Station 1. In general, the lowest plasma osmolalities were found in the spring at each station; the highest, in summer or fall. None of the season-to-season variations in plasma osmolality at Station 3 were significant.

The mean salinity was 27.6‰ at Station 1, 27.9‰ at Station 2, and 26.7‰ at Station 3. The total range of salinity measured was 22.9–30.4‰. The difference between stations for a single month was rarely more than 2‰. Bottom temperatures are summarized in Figure 2. In general, station-to-station differences were slight. Dissolved oxygen concentrations are presented in Figure 3. Station 3 tended to have a low oxygen concentration during the summer. During the cooler months, differences between stations in dissolved oxygen were less pronounced. Station 1 is 5.5 m deep; Station 2, 15.2 m; and Station 3, 10.7 m.

## Discussion

This investigation was undertaken in order to observe windowpane flounder blood chemistry in the field and to use a series of laboratory exposures in an attempt to explain the inter-station differences. However, the exposures actually provided only negative information on the causes of differences in blood chemistry observed in the field. The Interstate Sanitation Commission (unpubl.) reported a median copper concentration in the water column of western Long Island Sound of 12 μg/L; the highest reported copper levels were above 60 μg/L. This indicates that the exposure concentrations of 10 and 20 μg/L were realistic in terms of a polluted environment. Few water column cadmium concentrations were above 5 μg/L and the median was 1.0 μg/L. Therefore, the exposure concentrations of cadmium were realistic to slightly high. Mercury levels used in the exposures were high compared with those measured in Long Island Sound waters; the highest measured mercury concentration was 1.8 μg/L and the median was <0.1 μg/L, compared with exposure levels of 5.0 and 10.0 μg/L. The limited effects of mercury at a high exposure level and the lack of effects of cadmium and copper at more environmentally relevant water concentrations clearly demonstrated that the differences between stations cannot be explained by the effects of these metals. The lack of effects of the exposures in the present study does not diminish the possible usefulness of this type of approach. The exposures performed here were by no means comprehensive; a more extensive program of exposures might mimic the inter-station differences.

Bridges et al. (1976) reported changes in blood chemistry and, specifically, the development of anemia in winter flounder held in the laboratory for over 50 days. Anemia was not noted in such animals in the present study; hematocrits and hemoglobin levels of laboratory-held fish were typical of those of animals collected in the field during the same season. However, the plasma potassium levels of windowpane flounder used for the mercury exposure were somewhat higher than those of fish sampled immediately after collection; this may be the result of the length of time that the fish were held in the laboratory.

The geographical range of the field study was limited to stations at which monthly sampling was feasible. This limitation made it possible to describe seasonal

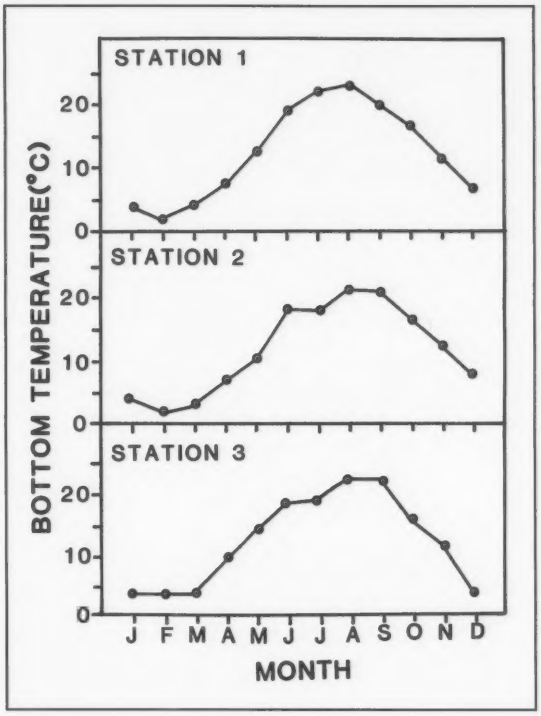


**Figure 2**
Yearly cycle of bottom temperatures at the three Long Island Sound stations. Each point is the mean of all samples taken from a given month and station throughout the study.

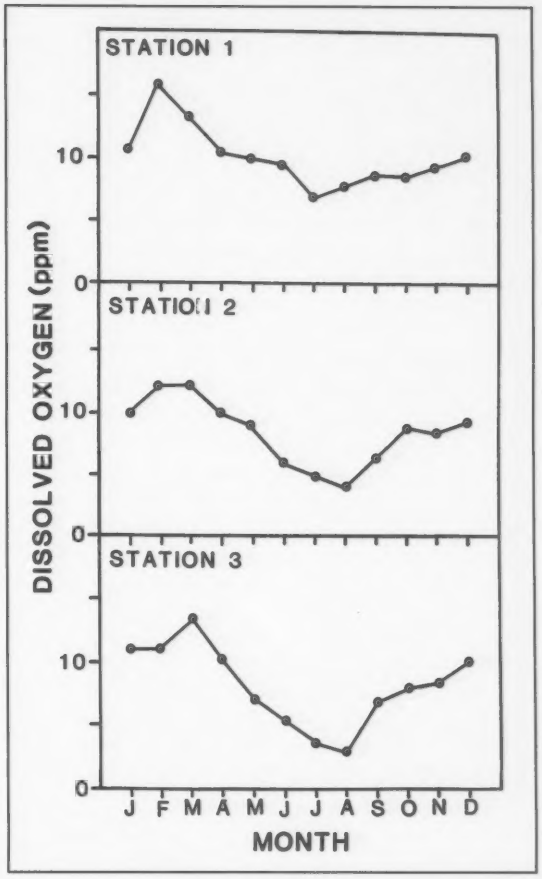


**Figure 3**
Yearly cycle of dissolved oxygen concentrations at the three stations in Long Island Sound. Each point is the mean of all samples taken from a given month and station throughout the study.

changes. Seasonal variations encompass a variety of parameters, including temperature, light, and nutrient availability. It was assumed that any variations which related to station rather than season were the result of differences in contaminant load. The low oxygen level at Station 3 during a portion of each summer may be indirectly a pollutant effect because low dissolved oxygen is often concomitant with organic pollution.

Mercury exposure produced more limited changes in windowpane flounder than in other species of fish exposed under similar conditions. Exposure to 10 μg/L mercury for 60 days produced no significant changes in the red cell component of windowpane flounder blood. Exposure of winter flounder *Pseudopleuronectes americanus* and striped bass *Morone saxatilis* to the same mercury concentration under similar conditions reduced hematocrit, hemoglobin, and red cell count by 18–48% of control values (Calabrese et al. 1975; Dawson 1979, 1982). The mercury-induced changes in plasma chemistry observed in this study paralleled those found in exposures of other species more closely than did the red cells. Both winter flounder and striped bass exhibited a significant increase in sodium and a decrease in calcium following mercury exposure, and winter flounder also had a drop in plasma calcium concentration (Dawson 1979, 1982). The lesser effects of mercury on the windowpane flounder suggest that this fish is generally less susceptible than striped bass or winter flounder or that the distribution of the metal within the animal differs from species to species. Pentreath (1976) reported that both gill and kidney accumulated high concentrations of mercury during the exposure of plaice *Pleuronectes platessa* L. to this metal. Accumulation in the gill and kidney would be likely to affect plasma chemistry; kidney accumulation may affect renal hematopoiesis as well.

This study produced no significant changes in windowpane flounder blood following copper exposure.

Other investigators have reported hematological effects of copper exposure in various fish species. Christensen et. al. (1972) reported significant increases in hematocrit and hemoglobin in the brown bullhead *Ictalurus nebulosus* following copper exposure. The exposure levels ranged from 27 to 107 μg/L, compared with our 10 and 20 μg/L, and the changes were noted in the fish exposed to 40–107 μg/L copper. It is possible that the lack of copper effects in the present study simply reflects a low exposure level.

The results of the cadmium exposure were similar to those obtained in an earlier exposure of the winter flounder *Pseudopleuronectes americanus*, to cadmium in this laboratory (Calabrese et al. 1975). In the earlier study, winter flounder were exposed for 60 days to 5 or 10 μg/L Cd, as were the windowpane flounder in the present study. No hematological changes were observed in winter flounder, although Na, K, and Ca were not measured. Larsson (1975) reported decreased hematocrits and hemoglobin concentrations following a 9-week exposure of the flounder *Pleuronectes flesus* L. to concentrations of cadmium as low as 5 μg/L. The same study demonstrated decreased calcium and potassium, but these were observed only at higher Cd concentrations.

Both the laboratory exposures and the field-sampling portion of this study suggest that the windowpane flounder is a hardy animal. The higher hematocrit and hemoglobin at the most polluted station compared with the least polluted station suggest an increase in hematopoiesis. The plasma osmolality, normally well below the osmolality of the surrounding water, was lower in fish collected from the most polluted station than in those collected from the cleanest station, indicating no loss of osmoregulatory ability. The limited effects of cadmium, copper and mercury exposures indicate that the species is not particularly vulnerable to these pollutants. These facts taken together suggest that the windowpane flounder at the most polluted station were subject to a stress, perhaps pollutant-induced, sufficient to challenge their metabolism, but a stress to which they were capable of adjusting.

## Acknowledgments

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# Reproduction, Movements, and Apparent Population Dynamics of the Atlantic Threadfin *Polydactylus octonemus* in the Gulf of Mexico*

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**Abstract.**–Trawl collections were made for Atlantic threadfin *Polydactylus octonemus* from 5 to 100 m in the Gulf of Mexico along a cross-shelf transect off Texas during October 1977–August 1981. Threadfin generally mature at 165–210 mm TL as they approach 7–9 months of age. Spawning primarily occurs in one period, mid-December–mid-March, and spans 45–120 days overall; 90% of successful spawning may occur in only 59% of that period. Threadfin in the northwestern Gulf range from <5 to 27 m depths in the demersal stage but are most abundant at <5 to 16 m. Young-of-the-year recruit in waters <5–16 m when 2–4 months old. Fish begin to disperse to deeper waters in early summer and form a positive size gradient from the estuaries seaward. Threadfin in the demersal phase are not abundant in the northwestern Gulf after 9–11 months of age and reach only 15 months there. Observed mean and predicted sizes were 135–165 mm TL at 6 months, 165–215 mm at 9 months, and 180–205 mm at 12 months. Fitted von Bertalanffy parameters were 2.17–2.92 ($K$, annual), 195–230 ($L_\infty$), and −0.03–0.08 years ($t_0$). Maximum size in the demersal phase is 230 mm TL in the northwestern Gulf, but more typically only 200–205 mm. Typical maximum life span ($t_L$) is about 1 year but may exceed that if individuals survive in a pelagic stage after spawning. Apparent mean time and cohort-specific total annual mortality rates are 97–100% in the northwestern Gulf. Population dynamics parameters presented are termed apparent because of the unknown effects of recruitment, movements, random variation, gear selectivity, etc. Spawning grounds seemingly lie along the Outer Continental Shelf, slope, or further offshore, and currents of the cyclonic shelf gyre off Texas and western Louisiana transport the young to estuarine and inshore nurseries.

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The Atlantic threadfin *Polydactylus octonemus* occurs along continental shelves from Massachusetts to Brazil, and in the Gulf of Mexico (Breder 1948, Briggs 1958, Dahlberg 1975, Fischer 1978). Although uncommon on the Atlantic coast (Hildebrand and Schroeder 1928, Anderson and Gehringer 1965, Anderson 1968, Wilk and Silverman 1976), it is abundant in Gulf of Mexico (Gulf) coastal, surf, and estuarine waters (Hildebrand 1954, McFarland 1963, Chittenden and McEachran 1976). However, its annual abundance seems to fluctuate greatly (Reid 1956, Gallaway and Strawn 1974, Ogren and Brusher 1977).

Despite its abundance, the life history of *P. octonemus* has not been studied in detail, and little supporting data have been published. General notes occur in many faunal studies including Gunter (1938a, 1945), Reid (1955), Miller (1965), and Juneau (1975). These notes indicate *P. octonemus* is a small, inshore species that occurs from spring through fall in the northern Gulf and spawns from fall through spring.

Our paper describes maturation, spawning periodicity, bathymetric distribution, recruitment, movements, age determination and growth using length frequencies, maximum size, life span, mortality, and relationships of length-weight, length-girth, standard-total length and fork-total length of *P. octonemus* in the northwestern Gulf. It also discusses spawning areas and larval dispersal in relation to Gulf hydrography, as well as how recruitment, movements, and randomization affect parameter estimation and interpretation.

## Materials and methods

Collections for *Polydactylus octonemus* were made from nearly 3000 trawl tows in 71 monthly or twice-monthly cruises, October 1977–August 1981, along a cross-shelf transect in the Gulf off Freeport, Texas (Fig. 1) aboard a chartered shrimp trawler. Gear used were twin 10.4-m (34-ft) trawls with a 4.4-cm stretched-mesh cod end and a tickler chain. Initial stations usually were located at depths of 9, 13, 16, 18, 22, 27, 36, and 47 m. Sampling was expanded to include stations at 5 and 24 m after November 1978 and at 55, 64, 73, 82,

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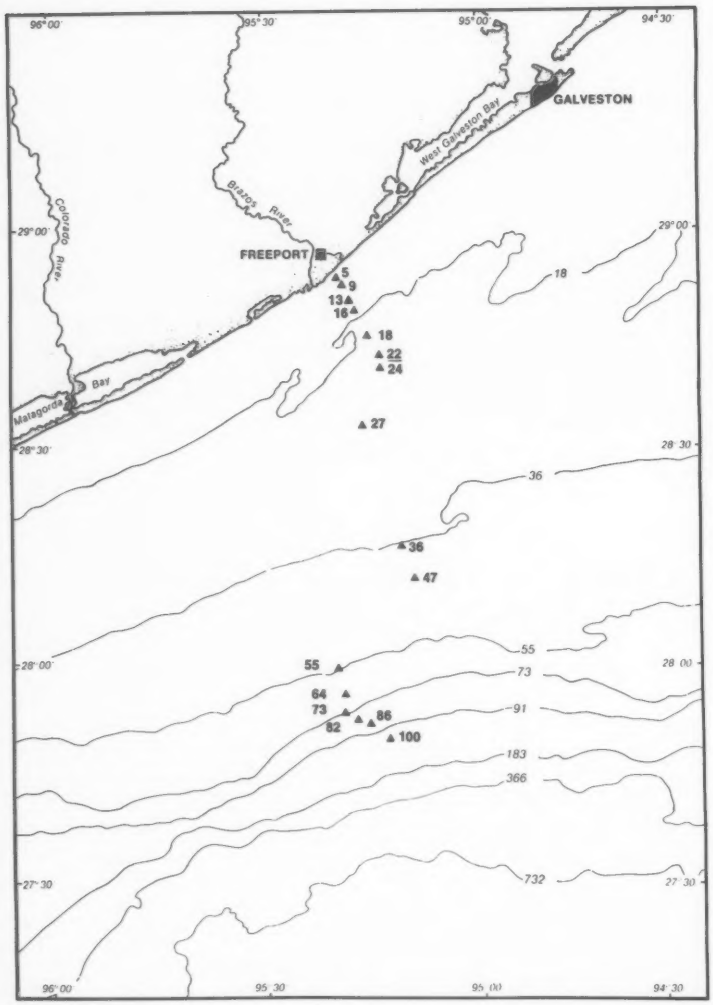



**Figure 1**
Location of sampling area off Freeport, Texas. Station depths and bathymetric contours are indicated in meters.

86, and 100 m after May 1979. Collections were made during the day through September 1978; thereafter, a day and a night cruise were usually made each month. Usually, two tows of 10 minutes bottom time were made at each depth, except that 8 were made at 16 m, 24 were made at 22 m, and only 1 tow was made at most depths prior to October 1978. We emphasize our spatial sampling design was a single, cross-shelf transect from a sampling frame that encompassed much of the northern Gulf.

All *P. octonemus* were culled from the catch, measured to the nearest millimeter total length, fixed in 10% formalin, and then preserved in 70% ethanol. All individuals collected January–December 1979 were processed to determine the following: total length (TL), fork length (FL), standard length (SL), girth at origin of the dorsal fin (G), total weight (TW), gonad weight (GW), and sex and gonad maturity stage. If available, 200 fish were randomly selected for similar processing in all other months, except standard length and girth were not recorded. Gonad maturity (Table 1) was determined by a modification of the Kesteven classification (Lagler 1978). Fish in the Early Developing and later stages were considered mature to calculate maturity curves (Bowering 1983), which indicate the length when half were mature ($M_{50}$). Gonadosomatic indices (GSI) were calculated for individual fish as: GSI = 100 GW/TW.

Age in years was determined by length-frequency analysis, e.g., the modal group progression analysis modification (Jearld 1983) of the Petersen Method (Lagler 1956). Knowing from this that essentially all

**Table 1**

Descriptions of gonad maturity stages assigned to *Polydactylus octonemus*.

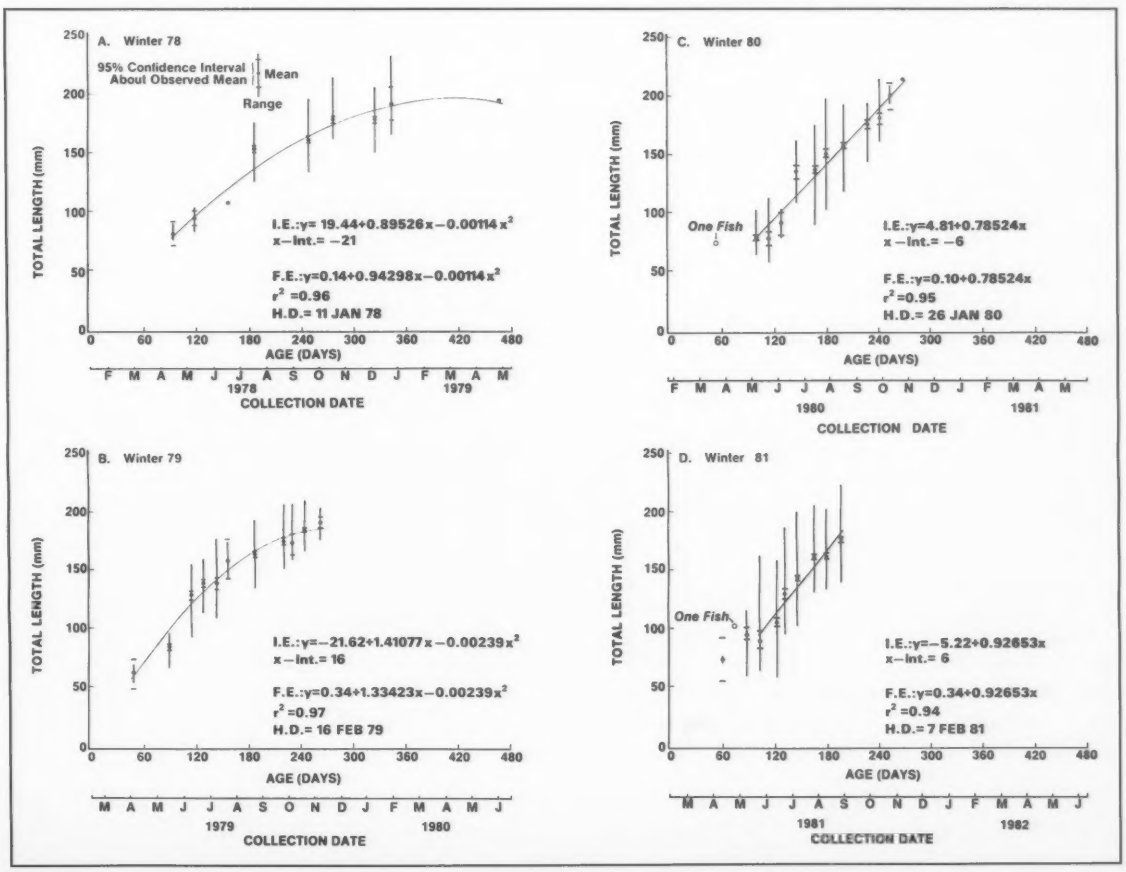
| Stage and name | Description |
|---|---|
| 1 Immature | Sex undetermined; gonads small or not visible. |
| 2 Maturing Virgin | Sex distinguishable; gonads thin, occupy <10% of body cavity; eggs not visible. |
| 3 Early Developing | Sex distinguishable to naked eye; gonads not flat, occupy 10–25% of body cavity; eggs opaque if present, not visible to naked eye. |
| 4 Late Developing | Gonads occupy 25–50% of body cavity; opaque eggs present, visible to naked eye. |
| 5 Gravid | Gonads occupy >50% of body cavity; up to 50% of eggs translucent. |
| 6 Ripe | Gonads occupy >50% of body cavity; >50% of eggs translucent. |
| 7 Spawning/Spent | Ovaries flaccid, completely or partially empty. |

fish were age 0, we forced through the origin a regression to approximate age in days at observed sizes; this procedure is detailed under the methods used to calculate hatching dates. Cohorts (year classes) were specified on length-frequency figures by the season and year when they were hatched, e.g., winter 1981. Arithmetic means were used to describe central tendencies of length for each cruise, because length frequencies within each cohort were generally normally distributed.

Descriptions of spawning periodicity (beginnings and ends) using length frequencies assumed the following size and age combinations predicted from regressions of total length on age (Fig. 2): 25–40 mm TL at 1

**Figure 2**

Mean observed and predicted sizes at age (days) for *Polydactylus octonemus* cohorts with a summary of the iterative process used to calculate final hatching dates (H.D.) and set time-scales for final growth equations (F.E.). Initial growth equations (I.E.) were scaled to a 1 February hatching date. All regressions are significant at $\alpha = 0.005$. The first two and three collections of the 1980 and 1981 cohorts, respectively, were deleted from calculations; see text on "Maturation and Spawning Periodicity" for explanation.



month, 45–70 mm at 2 months, 70–100 mm at 3 months, and 95–125 mm at 4 months, depending upon cohort. These sizes were reasonable because growth averaged 28–32 mm/30 days at 3–6 months of age in May–July (Dentzau 1985).

Apparent duration of the overall spawning period was approximated following Geoghegan and Chittenden (1982), as

$$\frac{\text{Time-specific mean size range early in life}}{\text{Mean growth/day early in life}}$$

Calculations were based on fish collected early in life, i.e., May–June; too few were collected before then (1–4 fish/cruise in March and April) to estimate growth. For the numerator, time-specific size range was estimated for each cohort as the mean of the 99% confidence intervals for observations in that period. For the denominator, individual growth increments were estimated as the difference between (1) observed mean total lengths on successive dates and (2) total lengths on successive dates predicted from regressions. Individual estimates of growth/day were then made as the individual growth increment divided by the time between collection dates. Mean growth/day early in life was then estimated as the average of individual growth/day values between successive collections during May–June. Dentzau (1985, table 3) details these calculations. Calculations were also made using 90% confidence intervals to compare how much successful spawning occurred in a period shorter than the overall period.

Hatching dates used to approximate time scales to calculate growth were determined by a one-step iteration process following Standard and Chittenden (1984). An initial hatching date of 1 February was used to start the approximation, because fish 50–90 mm, assumed to be 2–3 months old, first appeared in March–April. Quadratic regressions of total length on age in days after 1 February were then used as models to estimate an initial $\bar{x}$-intercept for each cohort; linear regression was used if the quadratic term was not significant at $\alpha = 0.05$. Final hatching dates were calculated by using the $\bar{x}$-intercept for each cohort to readjust the initial $x$-variable (time) scale, so each final growth curve passed through the origin (Fig. 2).

Recruitment patterns and movements in the Gulf were determined by analyzing length frequencies and catch-per-unit-effort against depth at specified "seasons" (months) of the year; length-frequency data from Galveston Bay, Texas (Gallaway and Strawn 1974), extended our analyses to estuaries. We use the words "recruit" and "recruitment" in two ways: (1) to describe movement to areas by young *P. octonemus* descending to the bottom from their pelagic early stages, and (2) horizontal movements from estuaries

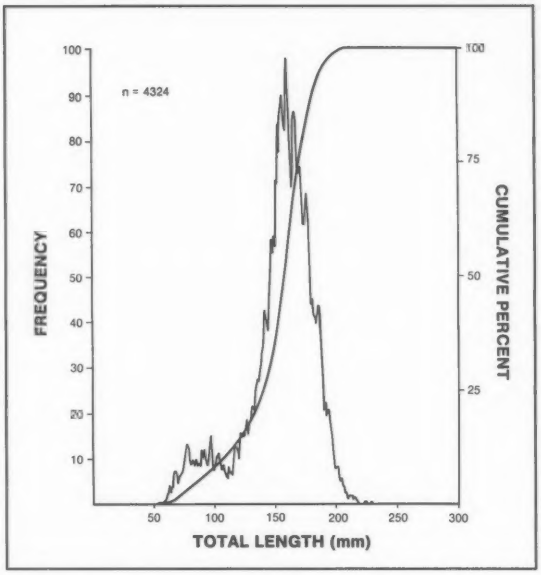



**Figure 3**
Length frequencies and cumulative percentage of all *Polydactylus octonemus* collected off Freeport, Texas, October 1977–August 1981.

to the Gulf, or within the Gulf, by fishes already in the exploited phase. The former conforms to Beverton and Holt's (1957) meaning of recruitment ($t_r$), because these areas are generally exploited, and to Beverton and Holt's (1957) and Ricker's (1975) meaning ($t_c$), because fish also then enter the exploited phase of life. Some gear selection for older, larger fish may occur as part of these processes.

Typical maximum life span was approximated by the Beverton-Holt model parameter $t_L$ (Gulland 1969), and typical maximum size was approximated as a corresponding length ($l_L$) following the definition that only 0.5–1.0% of the catch exceeds age $t_L$ (Alverson and Carney 1975, DeVries and Chittenden 1982). Values of $l_L$ were calculated from the cumulative frequency for all fish captured (Fig. 3). Specific values of $t_L$ were calculated from $l_L$ by solving for time in von Bertalanffy (Gulland 1969) and regression growth equations (Fig. 2).

Time and cohort-specific total annual mortality rates ($1 - S$) were calculated using $S = N_t/N_0$, where $S$ = rate of survival, and $N_t$ and $N_0$ are the numbers of fish at age each month or per tow. Observed estimates were compared against theoretical values calculated from the expression $\bar{Z} = 4.6/\text{number of years in life span}$ (Royce 1972:238). Total mortality rates, typical maximum life spans, maximum sizes, sizes at age, spawning period durations, and von Bertalanffy parameters

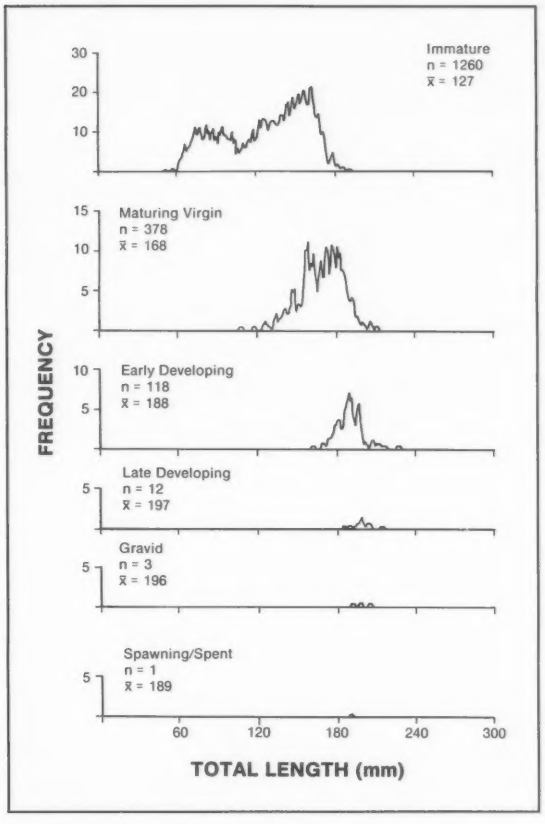



**Figure 4**
Length frequencies of immature and female *Polydactylus octonemus* by gonad stage.

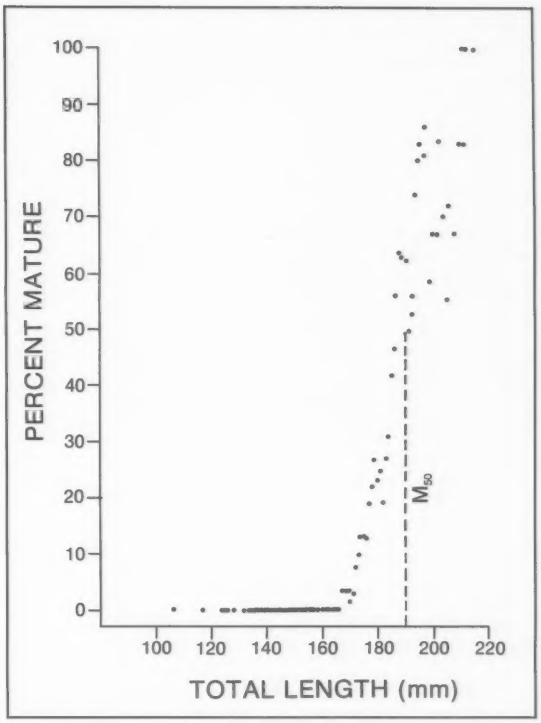



**Figure 5**
Percentage of mature female *Polydactylus octonemus* as a function of size.

presented were termed apparent, because they may have been affected by recruitment of larger young from estuaries to the Gulf, by emigration and/or gear avoidance of fish about age I, or by a change from demersal to pelagic behavior; if so, they overestimated mortality, $K$, and spawning period durations and underestimated life spans, maximum sizes, average sizes at age, and $L_\infty$.

Von Bertalanffy parameters were calculated using Fabens' (1965) program and the same data used in TL on age regressions (Fig. 2). These points described a curvilinear regression and evidenced an asymptote, so they met the minimum requirements for a von Bertalanffy fit (Knight 1968, Gallucci and Quinn 1979). Unless stated, all length frequencies were moving averages of three and all lengths were total length. The symbol "?L" was used for instances where the type of length was not reported. Conversions between standard, fork, and total lengths used regressions presented herein.

## Results

### Maturation and spawning periodicity

*Polydactylus octonemus* begin to mature at 165–210 mm in late summer–early fall. Sex usually could be determined by eye at 165 mm as many females entered the Early Developing stage (Fig. 4). Fish entered later stages at 180–210 mm. $M_{50}$ was 185–195 mm, about 7–9 months old (Fig. 5), in agreement with gonad-stage length frequencies.

Little somatic growth seemingly occurs after *P. octonemus* enter later stages of gonad development. Mean sizes were 188 mm in the Early Developing stage (Fig. 4), 197 mm when Late Developing, and 196 mm when Gravid. The only fish collected in the Spawning/Spent stage was 189 mm. Minimum and maximum sizes remained constant after the Early Developing stage.

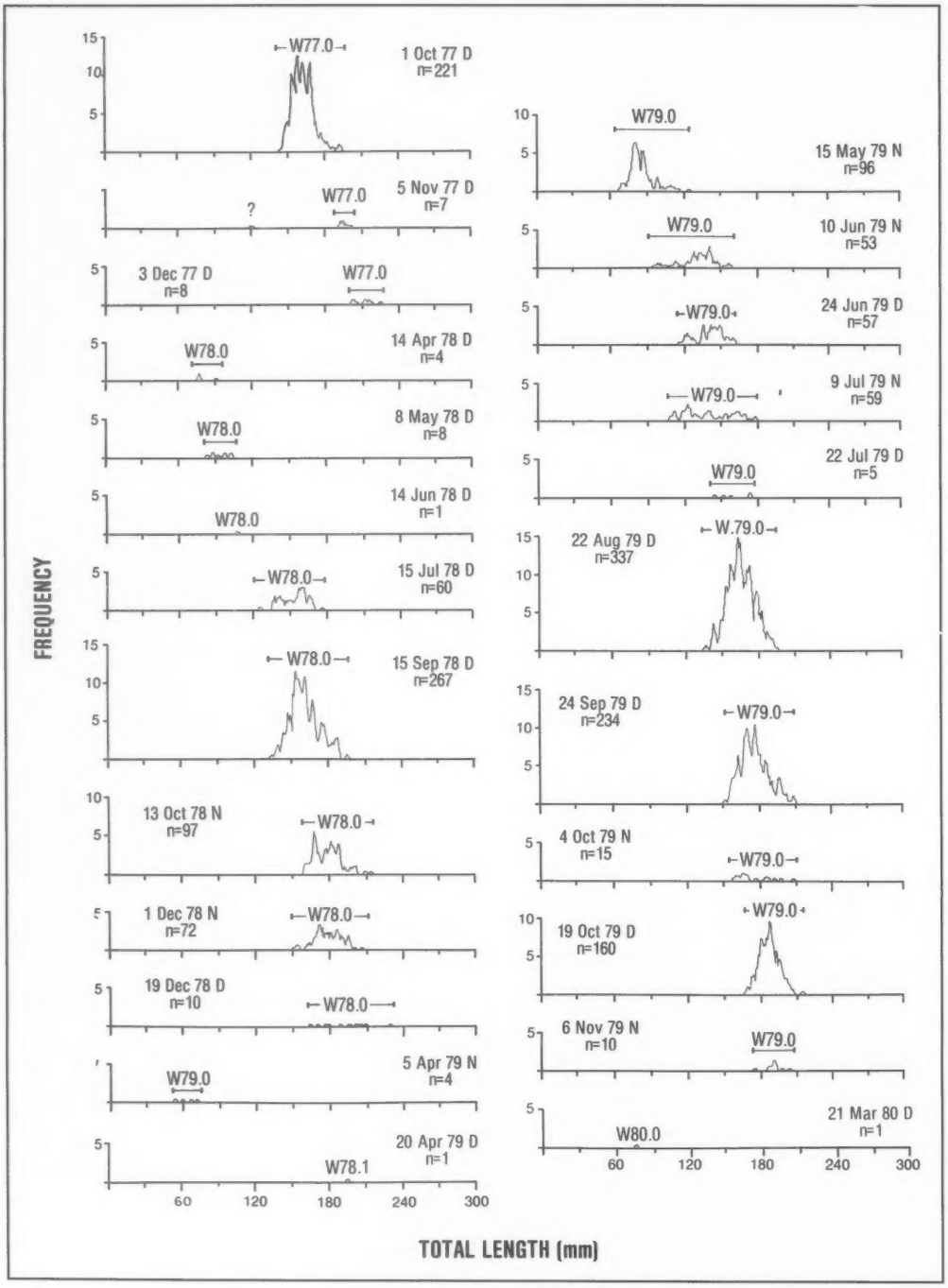



**Figure 6**

Monthly length frequencies of *Polydactylus octonemus* off Freeport, Texas, in day (D) and night (N) cruises. Bars in each panel depict cohort size ranges. The letter and first two digits above or within a bar indicate cohorts; the digit to the right of the decimal, age in years.

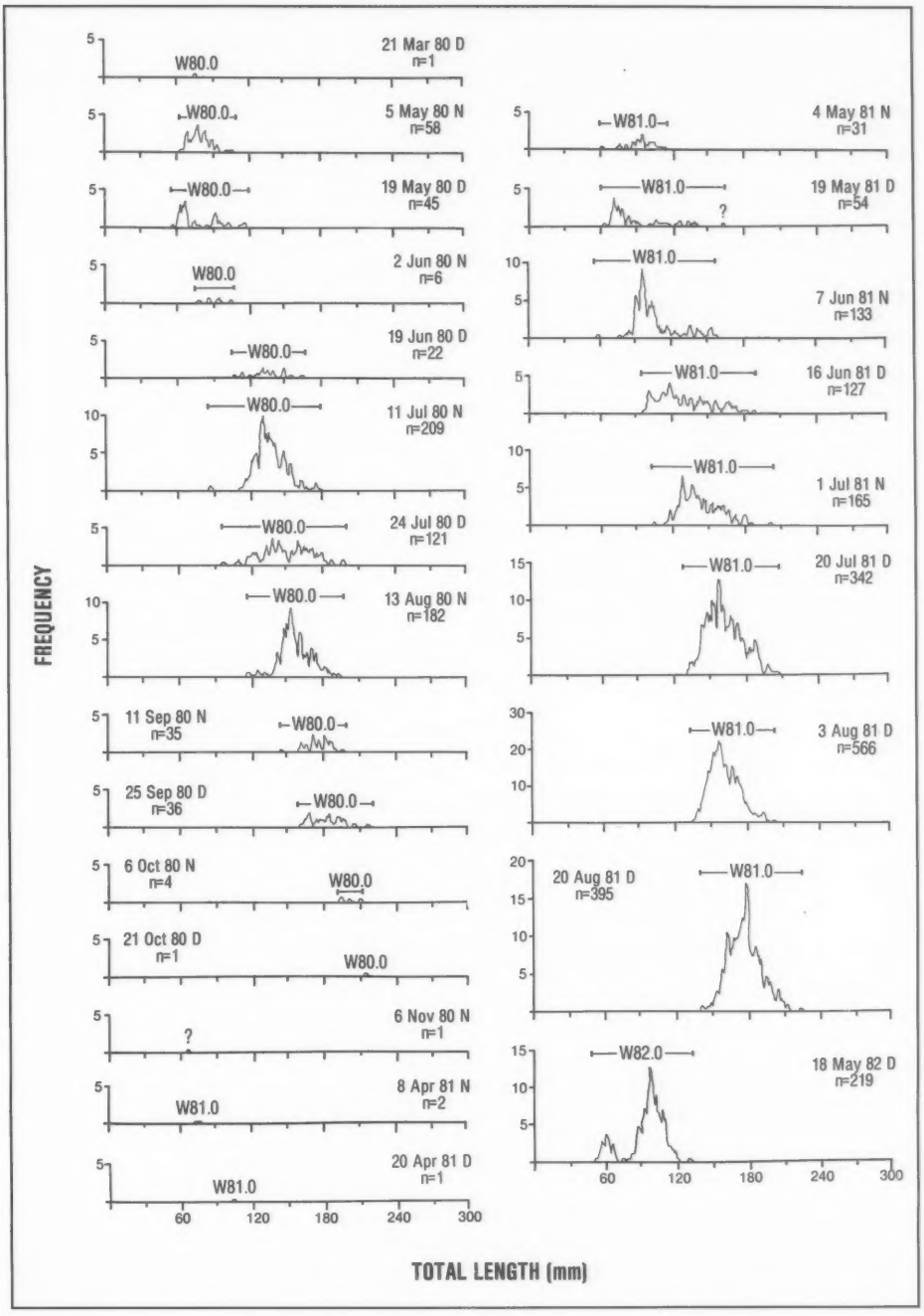



**Figure 6 (continued)**

*Polydactylus octonemus* primarily spawn in one discrete period from mid-December through mid-March. The well-defined modes in length frequencies from throughout the study (Fig. 6) suggest spawning occurred in one discrete period. Major spawning must have occurred during mid-December–mid-March, because small, young fish recruited mainly during mid-March–mid-May each year, e.g., fish 75–105 mm and

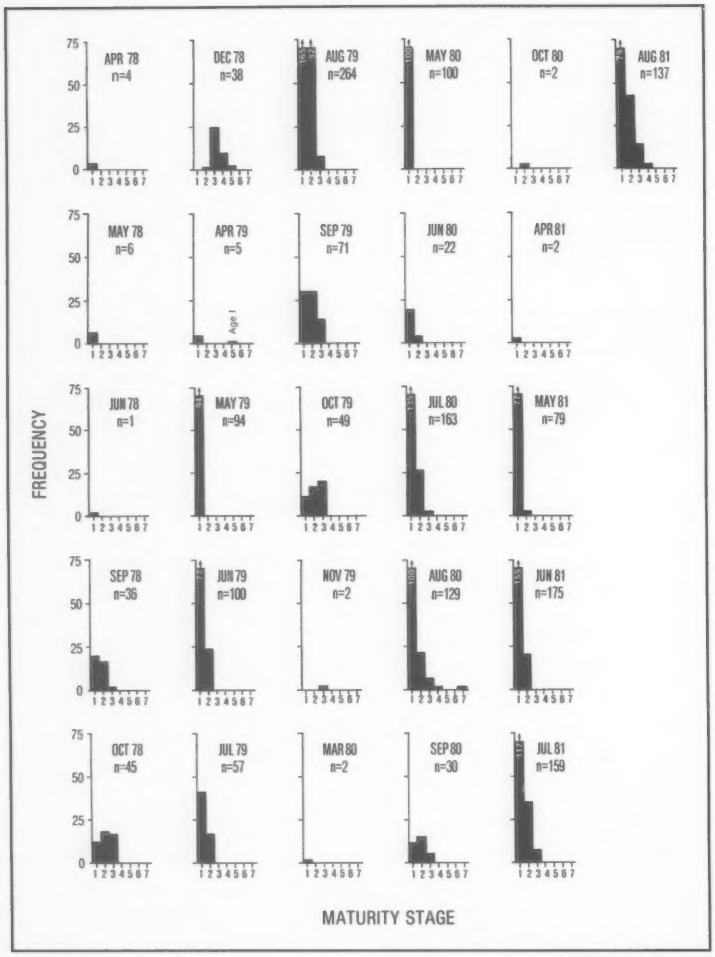



**Figure 7**
Monthly gonad maturity stages (defined in Table 1) of immature and female *Polydactylus octonemus*.

3–4 months of age recruited in abundance in mid-April–early May 1978, fish 50–70 mm and 2 months old in early April 1979, fish 65–115 mm and 2–4 months old in mid-May 1979, fish 75 mm and 3 months old in mid-March 1980, fish 55–115 mm and 2–4 months old in May 1980, and fish 60–115 mm and 2–4 months old in early April–early May 1981. Few fish 50–115 mm were collected from late August through February, indicating little spawning during late April–late October or November.

Calculated hatching dates were 11 January 1978, 16 February 1979, 26 January 1980, and 7 February 1981 for the 1978–1981 cohorts, respectively (Fig. 2). Other dates could have been calculated depending on data points included; however, the basic spawning period and coefficients of determination would be similar (Dentzau 1985). We deleted the earliest two collections in 1980 and earliest three in 1981 from calculations because mean sizes in these collections were as large or larger than those in subsequent ones and may have reflected incomplete recruitment or gear selection for larger fish, causing an upward size bias.

Gonad maturity data support the major mid-December–mid-March spawning period indicated by length frequencies. Except for one gravid age-I fish collected in April 1979, all fish collected in March–June were immature or maturing virgin (Fig. 7); none were in the Early Developing or later stages. Early and/or Late Developing stage fish were most common in October–December. Except for the one individual caught in April 1979, gravid fish were collected only in December as they approached age I. No ripe fish were collected, and few were gravid or late developing. Mean and/or maximum GSI values, although usually low, were high-

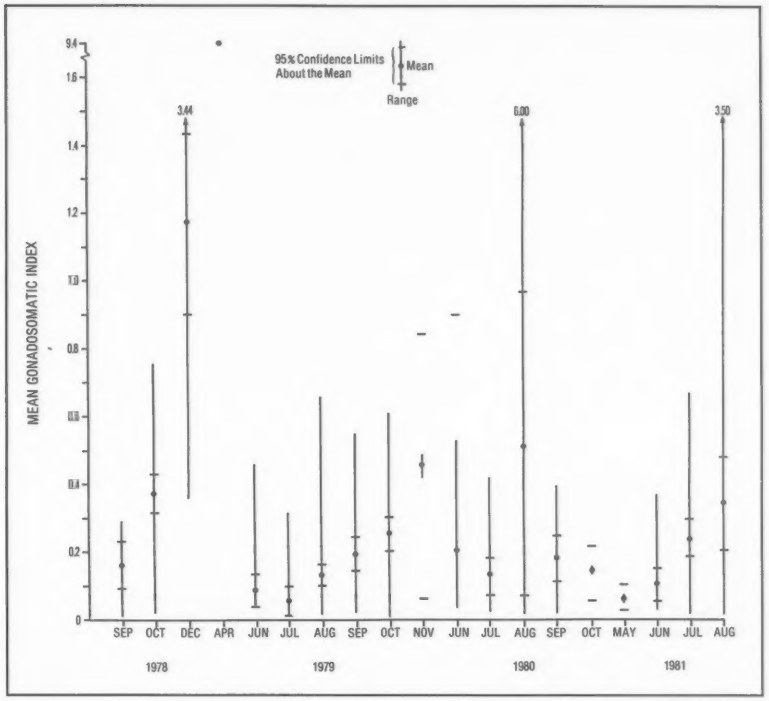



**Figure 8**
Monthly mean gonadosomatic indices, ranges, and 95% confidence limits about means for female *Polydactylus octonemus*, September 1978–August 1981.

est November–December (Fig. 8), except in August 1980 and 1981, when the few late-developing fish greatly skewed the means, and in mid-April 1979, when one age-I fish was gravid. The latter fish suggests some spawning in April and possibly May.

The apparent overall spawning period spans 45–120 days. Calculated overall spawning periods were 144 and 80 days in 1978, 53 and 80 days in 1979, 46 and 103 days in 1980, and 64 and 121 days in 1981 based on respective observed and predicted growth/day values. The broad 144-day interval for 1978 was based on only 9 fish and may be unreliable. Ignoring that value, spawning encompassed a 45–120 day interval which brackets the 90 day duration length frequencies indicated.

A large fraction of the successful spawning may occur in a period much shorter than the calculated overall spawning period duration. Using mean 90% instead of 99% confidence limits for observations, spawning periods were 78 and 43 days in 1978, 33 and 50 days in 1979, 27 and 60 days in 1980, and 40 and 76 days in 1981, based on respective observed and predicted growth/day values. On average, the duration estimated using 90% confidence limits was 59% of that using 99% limits. This suggests most spawning occurs in a relatively small part of the overall spawning period.

Cohorts are apparently produced by fish that first spawn when 10–14 months old, assuming the hatching dates and sizes at early age noted previously. Spawning at 10–14 months of age is supported by (1) the disappearance from collections of all but one fish sometime during late October–late December when 9–11 months old (Fig. 6), (2) the occurrence of large mean and maximum GSI values in October–December (Fig. 8), and (3) the collection of early developing and more sexually mature fish during September–December (Fig. 7).

*Polydactylus octonemus* exhibit a sex ratio of 1.00 male to 1.78 females. This ratio was observed in 800 fish and differed significantly from 1:1 ($\chi^2 = 64.98$, $\alpha = 0.05$, df = 1).

## Bathymetric distribution, recruitment, and movements

*Polydactylus octonemus* in the northwestern Gulf occur from <5 m depths to at least 27 m off Freeport. Only one specimen was collected deeper than 27 m, a 75-mm fish at 86 m in April, which may represent a pelagic young captured as the net was being retrieved. Greatest abundance generally occurred at 5 m, the shallowest depth occupied (Fig. 9), except in 1978 when this depth was occupied only in December, a time when

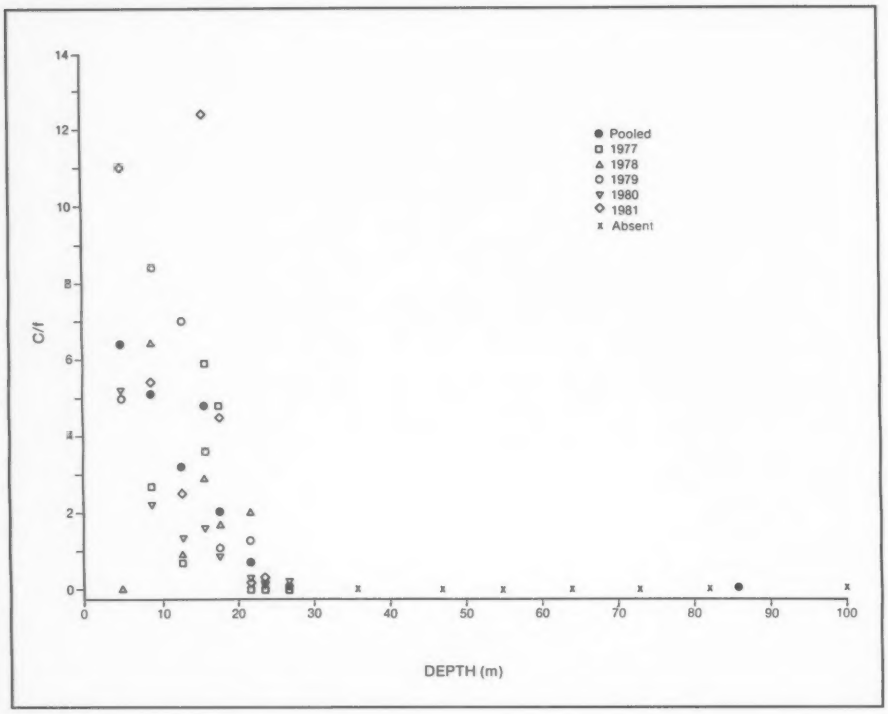



**Figure 9**
Catch/effort (mean number/10-min tow) by depth for *Polydactylus octonemus* off Freeport, Texas, each year and pooled, October 1977–August 1981. Tows in January and February were excluded in calculating effort because no fish were captured then.

fish had already begun to move offshore as noted below. Abundance was generally high at 9–16 m, although it often declined with increasing depth in this range. Abundance declined sharply between 18 and 22 m.

Young-of-the-year *P. octonemus* in the northwestern Gulf recruit to estuaries and coastal waters <5–16 m deep. Many young recruited to Galveston Bay in April and May when 50–110 mm (Fig. 10). In the Gulf, recruitment was greatest at the shallowest depths occupied. Fish 50–120 mm and 2–4 months old mainly recruited to 5–9 m in March–May, although some recruited as deep as 16 m (Fig. 11A, Table 2). Fish were most abundant at 5 m. Their abundance declined with increasing depth and was very low deeper than 13–16 m. Only one recruit was taken deeper than 16 m, the 75-mm fish at 86 m in April that may have been in a pelagic stage.

*Polydactylus octonemus* gradually disperse to deeper water in early summer and thereafter. Few age-0 fish were captured deeper than 9–13 m in April and May, but they were found at 18–27 m in June and were abundant at 16 m in July (Table 2). This gradual offshore dispersal is supported by the size gradient that existed seaward from Galveston Bay in June–December (Table 3), i.e., the smallest mean sizes were usually in Galveston Bay and the shallowest Gulf depths.

Larger *P. octonemus* lead the offshore dispersal. Minimum sizes were similar at each depth in the Gulf and in Galveston Bay during May (Fig. 10, 11A). In contrast, size compositions showed gradients of increasing size with depth in June, July, August, September, and October, suggesting larger, presumably older, fish move offshore first (Fig. 11A,B,C; Table 3).

Peak abundance of *P. octonemus* shifts towards deeper waters as they disperse offshore. Abundance was greatest by far at 5–9 m in May and June, then included 13 and 16 m in July as fish dispersed offshore (Table 2). Abundance peaked at 16 m in August and September, although fish were abundant from 5 or 9 to 18 m, and at 16–24 m in October (Table 2).

*Polydactylus octonemus* abandon estuaries and inshore portions of the Gulf (<5–9 m) in late fall and occupy only the offshore portions (13–24 m) before disappearing in November and December. Two fish at 9 m in November were the only individuals captured shallower than 13 m in the Gulf in November and December (Table 2), although peak abundance was at 5–9 m in May and June. Gallaway and Strawn's (1974) data show a similar abandonment of estuaries by late fall (Fig. 10).

*Polydactylus octonemus* were most abundant in July–September and least abundant November–April

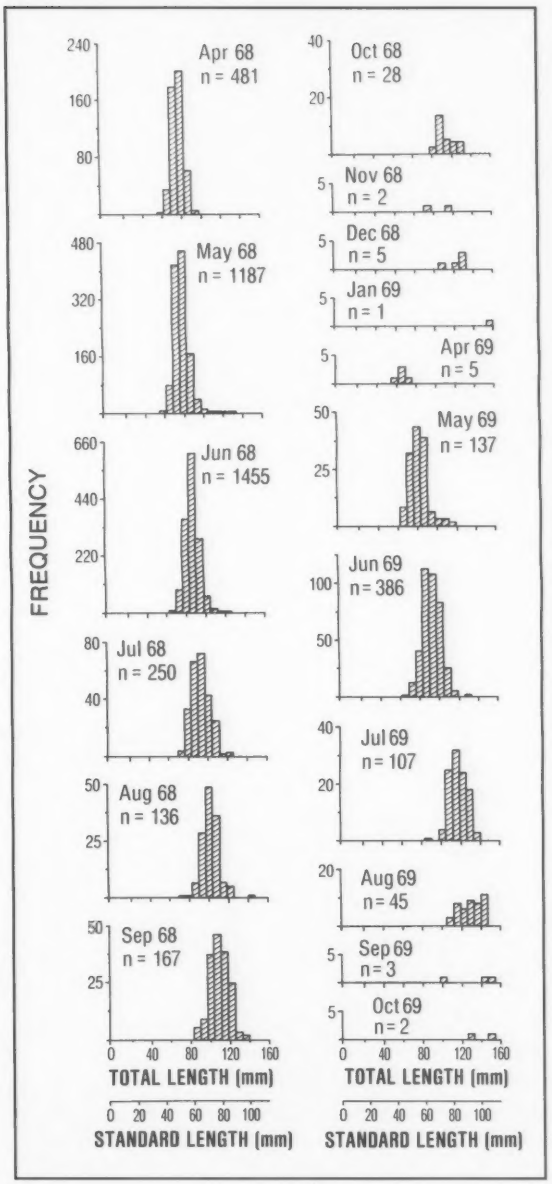

FREQUENCY
Apr 68 n = 481
Oct 68 n = 28
Nov 68 n = 2
Dec 68 n = 5
Jan 69 n = 1
Apr 69 n = 5
May 68 n = 1187
May 69 n = 137
Jun 68 n = 1455
Jun 69 n = 386
Jul 68 n = 250
Jul 69 n = 107
Aug 68 n = 136
Aug 69 n = 45
Sep 68 n = 167
Sep 69 n = 3
Oct 69 n = 2
TOTAL LENGTH (mm)
STANDARD LENGTH (mm)

**Figure 10**

Monthly length frequencies of *Polydactylus octonemus* in Galveston Bay, Texas, 1968 and 1969. Adapted from seine and trawl data of Gallaway and Strawn (1974); length frequencies are not moving averages of three.

(Fig. 12). Usually no *P. octonemus* were captured December–February.

## Age determination and growth

Only one cohort of *P. octonemus* usually occurs at any one time in the northwestern Gulf. The only exceptions to this we found were in April 1979 when two cohorts appeared, albeit on separate cruises, and possibly in November of 1977 and 1980 (Fig. 6), when the second cohort was represented by only one individual.

*Polydactylus octonemus* is not abundant in the demersal phase in the northwestern Gulf after 8–11 months of age and apparently reaches only 15 months. Cohorts were present only until their first November or December after which they were not captured again (Fig. 6), except for the 194-mm fish in April 1979 that was the only fish older than 12 months.

Apparent growth of *P. octonemus* varied between cohorts, but observed mean sizes, and von Bertalanffy and quadratic regression predictions, averaged 135–165 mm at 6 months, 165–215 mm at 9 months, and 180–205 mm extrapolated to 12 months (Table 4). Regardless of the growth model, for a given cohort, predicted sizes agreed within 6 mm or less at 6 and 9 months and within 11 mm at 12 months.

Fitted von Bertalanffy equations were:

$$(1978): l_t = 195.2[1-e^{-0.007999(t-30.40)}];$$

$$\text{annual } K = 2.92; \text{ annual } t_0 = 0.0833$$

$$(1979): l_t = 230.4[1-e^{-0.005955(t-11.69)}];$$

$$\text{annual } K = 2.17; \text{ annual } t_0 = -0.0320$$

where $l_t$ = TL in millimeters at time $t$ in days.

## Maximum size, life span, and mortality

*Polydactylus octonemus* in the demersal phase apparently reach a maximum size of about 230 mm in the northwestern Gulf but more typically only 200–205 mm. The largest of 4324 specimens collected was 229 mm; 99% were <202 mm and 99.5% were <206 mm (Fig. 3). The latter two sizes estimate an apparent $l_L$.

The apparent typical maximum life span in the demersal phase of *P. octonemus* in the northwestern Gulf is only 1 year. A value of $t_L = 1$ seems reasonable because (1) $l_L$ values of 202 and 206 mm can be substituted into hatching-date regressions and von Bertalanffy equations to predict values of 0.69–1.00 year; (2) observed and predicted mean sizes at 9 months are 165–215 mm and predicted sizes at 12 months are 180–205 mm; (3) the largest specimen was about 11 months old when collected in December 1978; and

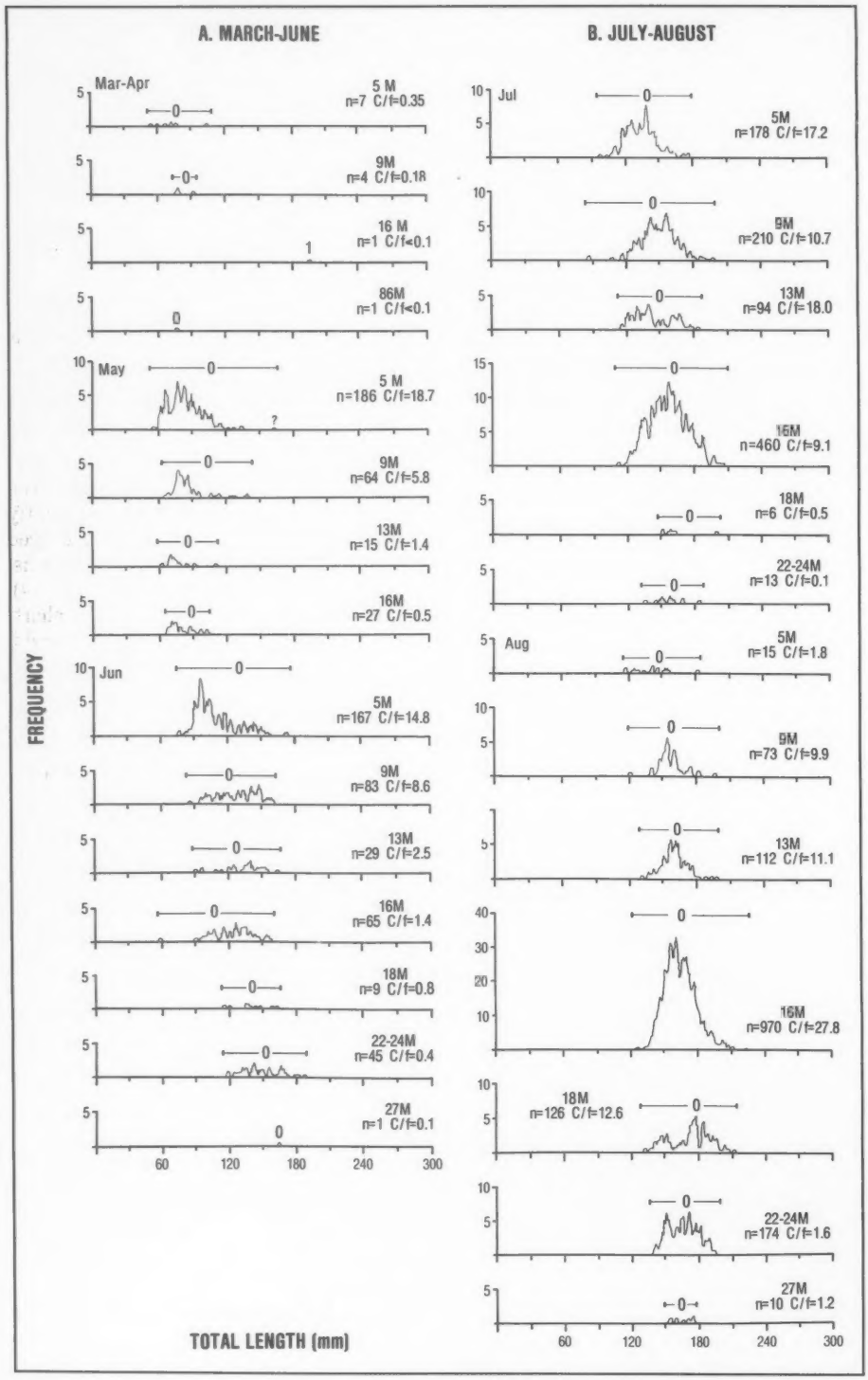



**Figure 11**
Length frequencies by depth for *Polydactylus octonemus* off Freeport, Texas, in March–June (A), July–August (B), September–October (C), and November–December (D). Data in each panel were pooled over the period October 1977–August 1981.

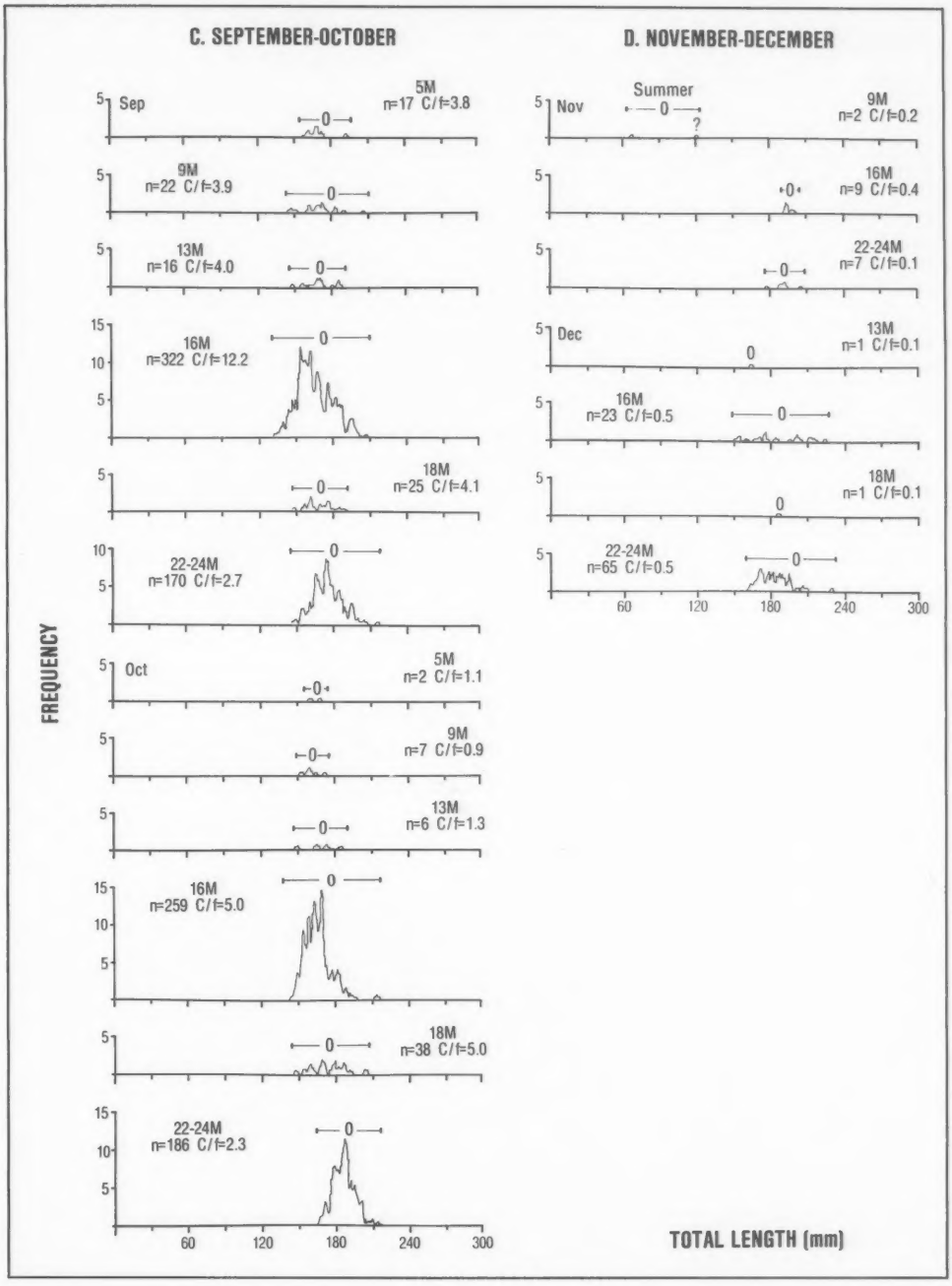



**Figure 11 (continued)**

(4) *P. octonemus* almost completely disappeared from trawl catches off Freeport at 9–11 months of age. The collection of one specimen seemingly 15 months old in April 1979 (Fig. 6) suggests a few age-I fish survive and remain in the white shrimp community, an inshore fauna described by Hildebrand (1954) and Chittenden and McEachran (1976). However, this would not greatly affect our estimate of $t_L$.

**Table 2**

Monthly catch/effort (mean number/10-min tow) of *Polydactylus octonemus* by depth off Freeport, Texas.

| | Depth (m) | | | | | | |
|---|---|---|---|---|---|---|---|
| Period | 5 | 9 | 13 | 16 | 18 | 22–24 | 27 |
| Mar.–Apr. | 0.4 | 0.2 | 0.1 | 0.1 | 0 | 0 | 0 |
| May | 18.7 | 5.8 | 1.4 | 0.5 | 0 | 0 | 0 |
| June | 14.8 | 8.6 | 2.5 | 1.4 | 0.8 | 0.4 | 0.1 |
| July | 17.2 | 10.7 | 18.0 | 9.1 | 0.5 | 0.1 | 0 |
| Aug. | 1.8 | 9.9 | 11.1 | 27.8 | 12.6 | 1.6 | 1.2 |
| Sep. | 3.8 | 3.9 | 4.0 | 12.2 | 4.1 | 2.7 | 0 |
| Oct. | 1.1 | 0.9 | 1.3 | 5.0 | 5.0 | 2.3 | 0 |
| Nov. | 0 | 0.2 | 0 | 0.4 | 0 | 0.1 | 0 |
| Dec. | 0 | 0 | 0.1 | 0.5 | 0.1 | 0.5 | 0 |

*Polydactylus octonemus* in the demersal phase have an apparent total annual mortality rate off Texas that approaches 100%, mean time- and cohort-specific values being 97–100%. Only one winter cohort was present in 31 of 32 months off Freeport (Fig. 6), so time-specific estimates were 100% in each of these instances. Cohort-specific values were 100% in 6 of 7 months for 1978, 8 of 8 months for 1979, and 5 of 5 months for 1980 fish because $N_t$ was zero. A time-specific estimate for April 1979 and a cohort-specific estimate for the 1978 cohort in April of 1978 and 1979 were 75% and 95% ($Z = 1.39$ and 3.00), respectively, but the former value may be an underestimate because the younger cohort was incompletely recruited in April.

**Table 3**

Mean total length (mm) for *Polydactylus octonemus* in Galveston Bay, 1968 and 1969 (adapted from Gallaway and Strawn 1974), and by depth in the Gulf off Freeport, Texas. Data at each depth in the Gulf are for age-0 fish pooled over the period October 1977–August 1981.

| | Galveston Bay | | Gulf of Mexico (depth in m) | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Month | 1968 | 1969 | 5 | 9 | 13 | 16 | 18 | 22–24 | 27 | 86 |
| Mar. | | | 74.0 | | | | | | | |
| Apr. | 77.2 | 65.7 | 70.7 | 80.5 | | | | | | 75.0 |
| May | 78.3 | 81.6 | 84.9 | 86.7 | 76.9 | 80.7 | | | | |
| June | 86.6 | 92.7 | 109.4 | 127.1 | 132.1 | 123.2 | 139.2 | 147.7 | 164.0 | |
| July | 93.1 | 117.5 | 133.6 | 148.6 | 142.8 | 156.4 | 163.5 | 157.0 | | |
| Aug. | 102.3 | 129.5 | 140.6 | 157.1 | 159.9 | 164.5 | 173.4 | 165.5 | 164.9 | |
| Sep. | 109.7 | 132.0 | 168.2 | 169.4 | 168.5 | 164.7 | 168.8 | 175.7 | | |
| Oct. | 114.1 | 140.3 | 163.0 | 160.1 | 167.2 | 165.0 | 173.6 | 185.5 | | |
| Nov. | 104.8 | | | | | 194.7 | | 189.7 | | |
| Dec. | 123.9 | | | | 164.0 | 185.9 | 186.0 | 181.8 | | |
| Jan. | 158.0 | | | | | | | | | |

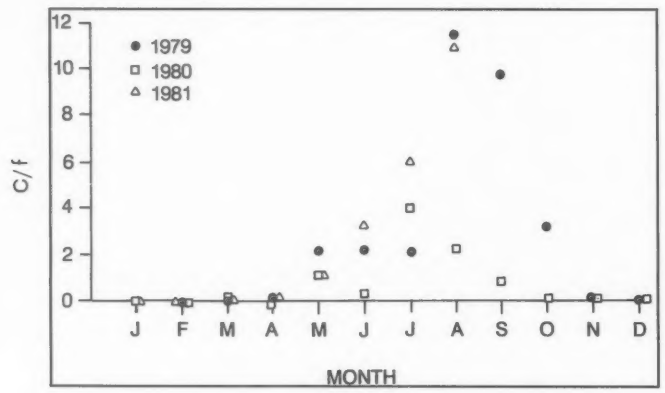



**Figure 12**

Catch/effort (mean number/10-min tow) by month of *Polydactylus octonemus* off Freeport, Texas, each year.

**Table 4**

Observed mean sizes (mm TL), size ranges, and predicted sizes by hatching-date regressions (Fig. 2) and von Bertalanffy models for 1977–80 *Polydactylus octonemus* cohorts at 6, 9, and 12 months of age. Observed values are pooled data from July–August at 6 months and October–November at 9 months. Dentzau (1985, table 4) gives more detail.

| | Observed sizes | | | |
|---|---|---|---|---|
| | 6 mo | | 9 mo | |
| Year | Mean | Size range | Mean | Size range |
| 1977 | — | — | 178 | 144–200 |
| 1978 | 153 | 125–176 | 178 | 160–214 |
| 1979 | 154 | 107–194 | 183 | 157–212 |
| 1980 | 148 | 86–197 | 207 | 194–214 |
| 1981 | 160 | 103–223 | — | — |

| | Predicted sizes | | | | | |
|---|---|---|---|---|---|---|
| | 6 mo | | 9 mo | | 12 mo | |
| | Regression | von Bertalanffy | Regression | von Bertalanffy | Regression | von Bertalanffy |
| 1978 | 133 | 136 | 172 | 166 | 192 | 181 |
| 1979 | 163 | 157 | 186 | 187 | — | 205 |
| 1980 | 141 | — | 212 | — | — | — |

**Table 5**

Total weight–total length, girth–total length, and length–length regressions for *Polydactylus octonemus* with supporting statistics. All regressions were significant at $\alpha = 0.05$. The symbol $v$ is from Ricker's (1973) GM regression. Measures are grams and millimeters. See Methods for symbols.

| Equation | $n$ | Range | $100r^2$ | $v$ |
|---|---|---|---|---|
| $\text{Log}_{10}$ TW = −5.72 + 3.27 $\text{Log}_{10}$ TL (males + females + immatures) | 2398 | 51–226 | 99.0 | 3.29 |
| $\text{Log}_{10}$ TW = −6.29 + 3.53 $\text{Log}_{10}$ TL (males + females) | 800 | 107–226 | 94.2 | 3.64 |
| $\text{Log}_{10}$ TW = −6.50 + 3.63 $\text{Log}_{10}$ TL (males) | 286 | 126–207 | 92.8 | 3.76 |
| $\text{Log}_{10}$ TW = −6.25 + 3.51 $\text{Log}_{10}$ TL (females) | 514 | 107–226 | 94.8 | 3.60 |
| TL = 15.10 + 1.70 G | 847 | 51–226 | 94.8 | 1.74 |
| G = −4.22 + 0.56 TL | 847 | 51–226 | 94.8 | 0.57 |
| TL = −1.04 + 1.42 SL | 847 | 51–226 | 99.1 | 1.43 |
| SL = 1.74 + 0.70 TL | 847 | 51–226 | 99.1 | 0.70 |
| TL = −2.77 + 1.26 FL | 2398 | 51–226 | 99.5 | 1.27 |
| FL = 2.80 + 0.79 TL | 2398 | 51–226 | 99.5 | 0.79 |

### Weight, girth, and length relationships

Total weight–total length regressions for males and females (Table 5) were not significantly different in slope ($F = 2.91$, df = 1, 798), but they differed in elevation ($F = 7.73$, df = 1, 799). Therefore, equations are presented for each sex and for males and females pooled. Total weight–total length regressions for all fish and for males and females pooled were significantly different in slope ($F = 99.10$, df = 1, 2056); however, the one equation that pools all fish may be useful at this stage of management.

## Discussion

### Spawning periodicity

The primary winter–spring spawning period we found for *Polydactylus octonemus* in the northwestern Gulf,

**Table 6**

Available information on larval, young (see text footnotes 1 and 4), and juvenile specimens of *Polydactylus octonemus* collected in western Gulf of Mexico surface waters by plankton net, dip net, meter net, and neuston net. Reference numbers correspond to locations in Figure 13.

| Reference number | Location collected (lat.°N) | (long.°W) | Collection date | Depth (m) | Length (mm) | Reference |
|---|---|---|---|---|---|---|
| | | | **Texas and Louisiana** | | | |
| 1 | Gulf off Barataria Bay, Louisiana | | Apr. 33 | <22 | 50 TL | Gunter 1938b |
| 2 | 26°40′ | 92°00′ | 8 May 54 | 1602 | — | Springer and Bullis 1956 |
| 3 | 26°05′ | 95°25′ | 27 May 54 | 1890 | — | Springer and Bullis 1956 |
| 4 | 26°15′ | 95°00′ | 7 Mar. 65 | ≅2300 | 44–54 TL | Pequegnat (text footnote 3) |
| 5 | 27°52′ | 93°48′ | Mar. 72 | 137 | 57–71 TL | Bright and Cashman 1974 |
| 6 | 27°33′ | 96°06′ | Jan.–Feb. 76 | 134 | 35–36 TL | Pequegnat et al. 1977 |
| 7 | 26°57′ | 96°32′ | Jan.–Feb. 76 | 106 | 38–47 TL | Pequegnat et al. 1977 |
| 8 | 26°10′ | 96°24′ | 27 Feb. 76 | 91 | 21–52 TL | Pequegnat et al. 1977 |
| 9 | 27°17′ | 96°23′ | 25 Mar. 76 | 131 | 40 TL | Pequegnat et al. 1977 |
| 10 | 27°30′ | 96°44′ | 8 Apr. 76 | 49 | 56 TL | Pequegnat et al. 1977 |
| 11 | 27°17′ | 96°23′ | 10 Apr. 76 | 131 | 43–80 TL | Pequegnat et al. 1977 |
| 12 | 26°58′ | 97°11′ | 29 May–8 June 76 | 25 | — | Pequegnat et al. 1977 |
| 13 | 27°17′ | 96°23′ | 20 Apr. 77 | 131 | 65–72 TL | Wormuth et al. 1979 |
| 14 | 27°34′ | 96°07′ | 15–21 May 77 | 134 | — | Wormuth et al. 1979 |
| 15 | 26°10′ | 96°24′ | 15–21 May 77 | 91 | — | Wormuth et al. 1979 |
| 16 | Gulf off Freeport | | 6 May 79 | 54 | 56–66 TL | Rockett[1] |
| 17 | 28°14′ | 94°57′ | 23 Apr. 59 | 47 | — | Bullis and Thompson 1965 |
| 18 | 26°00′ | 96°00′ | 22 Apr. 82 | 200 | 44 SL | Lieby[2] |
| 19 | 26°30′ | 94°30′ | 24 Apr. 82 | 200 | 39–51 SL | Lieby |
| 20 | 27°00′ | 92°00′ | 25 Apr. 82 | 200 | 40–48 SL | Lieby |
| 21 | 27°30′ | 92°30′ | 10 May 82 | 200 | 41–44 SL | Lieby |
| 22 | 27°30′ | 93°30′ | 10 May 82 | 200 | 45 SL | Lieby |
| 23 | 28°00′ | 94°00′ | 9 May 82 | 58 | 38–45 SL | Lieby |
| | | | **Mexico** | | | |
| 24 | 20°01′ | 92°27′ | 14 May 54 | 1467 | — | Springer and Bullis 1956 |
| 25 | 19°13′ | 95°34′ | 17 May 54 | 1260 | — | Springer and Bullis 1956 |
| 26 | 20°34′ | 95°37′ | 20 May 54 | 2160 | — | Springer and Bullis 1956 |
| 27 | 21°42′ | 93°35′ | 22 May 54 | 2736 | — | Springer and Bullis 1956 |
| 28 | 24°00′ | 96°50′ | 25 May 54 | 1035 | — | Springer and Bullis 1956 |
| 29 | 24°54′ | 96°05′ | 27 May 54 | 1530 | — | Springer and Bullis 1956 |
| 30 | 25°08′ | 94°58′ | 9 Mar. 65 | — | 48 TL | Pequegnat (text footnote 3) |
| 31 | 23°14′ | 96°08′ | 23 Apr. 75 | — | 49–60 TL | Kennicutt (text footnote 3) |
| 32 | 23°00′ | 96°52′ | 24 Apr. 75 | — | 53–66 TL | Kennicutt (text footnote 3) |
| 33 | 20°40′ | 92°55′ | 25 Nov. 56 | 2088 | — | Bullis and Thompson 1965 |
| 34 | 20°40′ | 96°05′ | 2 Apr. 56 | 1782 | — | Bullis and Thompson 1965 |
| 35 | 19°35′ | 95°28′ | 11 Apr. 56 | 2300 | — | Bullis and Thompson 1965 |

[1]M. Rockett, Appalachian State Univ., Boone, NC 28608, pers. commun., March 1981.
[2]M. Lieby, Bur. Mar. Res., St. Petersburg, FL 33701, pers. commun., Feb. 1986.

mid-December–mid-March and continuing at a lower level through April or May, generally agrees with the limited literature. Gunter (1938b, 1945) suggested fall–winter or late winter–early spring spawning, because 28–100 mm young appeared from April through June. Winter–spring spawning is also supported by: (1) collection of neustonic "larvae"[1] 21–80 mm[2] in water 25–134 m deep over the south Texas continental shelf primarily from mid-January through early April, but also into early June (Pequegnat et al. 1977); (2) collection at the surface of fish (a) 44–54 mm in water 2300 m deep in early March off south Texas (26°15′N, 95°00′W)[3], (b) 57–71 mm (41–51 mm SL) in water 137

[1]Larvae as used by Pequegnat et al. (1977) and Wormuth et al. (1979) may encompass the juvenile stage defined by Moyle and Cech (1982).
[2]We obtained sizes from specimens deposited at the Texas Cooperative Wildlife Collection (TCWC), Texas A&M University, College Station, TX.
[3]Fish were collected by W. Pequegnat and M. Kennicutt (Dep. Oceanogr., Texas A&M Univ.), and deposited in TCWC.

m deep in March over the West Flower Garden Bank off Texas (27°52′N, 93°48′W; Bright and Cashman 1974), (c) 50 mm in water <22 m in April off Barataria Bay, LA (Gunter 1938b), and (d) 56–66 mm in water 54 m deep in early May off Freeport (M. Rockett, Appalachian State Univ., Boone, NC 28608, pers. commun., March 1981); (3) collection at the surface in early May of "young"[4] off south Texas (26°05′N, 95°25′W) and off the Louisiana continental shelf (26°40′N, 92°00′W) in water 1890 and 1602 m deep, respectively (Table 6; Springer and Bullis 1956); and (4) collection of neustonic "larvae" (footnote 1) 65–72 mm in water 91–134 m deep in mid-April–mid-May off south Texas (Wormuth et al. 1979).

Our calculated spawning-period duration of 45–120 days assumes large fish hatch before small ones and all grow at the same rate (Geoghegan and Chittenden 1982). The latter assumption appears reasonable, because 99% confidence intervals for observations (in Dentzau 1985, table 3) were fairly constant between cruises within each May–June period. Our calculated duration may be an overestimate because continued recruitment of small fish to the Gulf would tend to depress estimates of mean growth/day, the denominator in our spawning-duration equation. The numerator, mean size range, is less affected; larger recruits gradually disperse offshore to deeper waters, but we collected throughout and beyond the bathymetric range of the species. Comparisons of spawning-period durations from 90 and 99% confidence intervals are valid, however; such calculations use the same values except $t$.

Our calculated hatching dates indicate mid-January–mid-February spawning, these being mean spawning dates because regression predicts averages. They are in error to the extent that regression curves do not pass through the origin and that they are asymptotic to the $x$- or $y$-axis in very early life. The latter is an unknown; the former problem does not seem serious, because Shirota (1970, in Hunter 1981) found length at first feeding in many species is four times the egg diameter. Egg diameter is not known in *P. octonemus* (Martin and Drewry 1978, deSylva 1984), but it averages 0.76 mm in the closely related *Eleutheronema tetradactylum* (deSylva 1984). This suggests *P. octonemus* is 3–3.5 mm at hatching, so only a few days error occurs in $x$, at most.

## Spawning areas

Any spawning of *P. octonemus* in the northern or northwestern Gulf presumably occurs in the water column. Our data and the literature (Chittenden and McEachran 1976; Wohlschlag et al. 1977, 1979) indicate they basically disappear as demersal fish from the white and brown shrimp communities of the northern Gulf in November–December. They may assume a pelagic behavior then, which would explain their apparent absence in January–February, because Hastings et al. (1976) observed this species in December in habitat typical of pelagic fish—open water areas around an offshore platform in water 18 m deep in the northeastern Gulf off Panama City, Florida.

Catch records for young in the literature and the disappearance of *P. octonemus* from the white and brown shrimp communities in their primary winter spawning period, if the latter does not simply reflect gear selectivity following assumption of a pelagic habit, suggest this species spawns along the outer continental shelf, the continental slope, or further offshore. Although pelagic "larvae" (footnote 1) and juveniles have been collected at the surface in or near waters of the white shrimp community off Texas and Louisiana in April–early June (collections 1 and 12, Fig. 13) or the brown shrimp community in late February–May (collections 8, 10, 15, 16, and 23, Fig. 13), more frequent collections in U.S. waters have been made along the outer continental shelf at 106–137 m in January–May (collections 5, 6, 7, 9, 11, 13, and 14, Fig. 13), and even further offshore at ≥200–2300 m in March-May (collections 2, 3, 4, 18, 19, 20, 21, and 22, Fig. 13). Several collections of "young" (footnote 4) and juveniles have been made in Mexican waters 1035–2736 m deep between Laguna Madre Tamaulipas and Campeche Bank in March–May (collections 24–32, Fig. 13). Similarly, young of other *Polydactylus* spp. also occur off continental shelves although adults are common in inshore waters; e.g., Klawe and Alverson (1964) found young *P. opercularis* and *P. approximans* <48 mm 250 nm offshore in the eastern tropical Pacific Ocean.

In contrast to the abundance of *P. octonemus* larvae and juveniles in the western and northwestern Gulf, they have not been identified in extensive collections off the west coast of Florida from Pensacola on the north, south to the Florida Keys (Vick 1964; Houde et al. 1979; M. Lieby, Bur. Mar. Res., St. Petersburg, FL 33701, pers. commun., Feb. 1986). This suggests little or no spawning in that area and in the eastern side of the Loop Current, which contributes water to the western Florida shelf (Austin and Jones 1974).

*Polydactylus octonemus* eggs, larvae, and juveniles, pelagic like other polynemids (Breder and Rosen 1966, Kagawade 1970), presumably use current transport to reach their estuarine and shallow Gulf nurseries. Standard and Chittenden (1984), based on Murphy and Chittenden (unpubl.), suggested spawning in *Larimus fasciatus* and other Gulf fishes is timed to coincide with

[4]Springer and Bullis (1956) defined young as postlarval, juvenile, and young specimens.

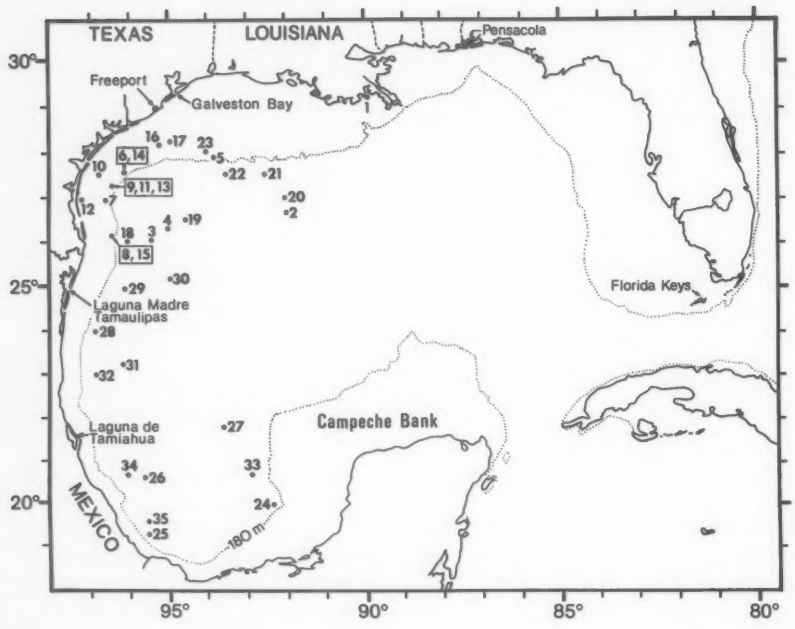



**Figure 13**
Summary of available collections of larval, young (see text foonotes 1 and 4, and juvenile *Polydactylus octonemus* from surface waters in the Gulf of Mexico. Reference numbers correspond to those in Table 7 where collection information is given.

the occurrence of downcoast alongshore coastal currents (towards Mexico) and onshore surface Ekman transport caused by downcoast wind stress along much of the Texas and western Louisiana coast from August–September through April–May (Kelly et al. 1981). When alongshore currents are downcoast, an eastward or northeastward counterflow along the shelf break forms a cyclonic gyre on the continental shelf off Texas and western Louisiana (Kelly et al. 1984). The alongshore components of this gyre probably transport, in merry-go-round fashion, eggs, larvae, and juvenile *P. octonemus* from the outer shelf and slope to their shallow nurseries. Portions of this current not diverted westward at the Mississippi Delta (Kelly et al. 1983) may carry eggs and larvae east towards the west coast of Florida where older stages of *P. octonemus* have been collected in the surf and estuaries (Powell et al. 1972, Ogren and Brusher 1977) even though, as noted, larvae have not been found. Shaw et al. (1985) suggested a similar model for Gulf menhaden *Brevoortia patronus*.

Onshore surface Ekman transport components of the gyre seemingly could transport young *P. octonemus* directly inshore in the northwestern Gulf; however, this does not seem to be the case. Unlike *P. octonemus*, fishes of the brown shrimp community which spawn offshore and have pelagic eggs and larvae do not appear to be transported into the white shrimp community; they are basically absent there (Chittenden and McEachran 1976).

Depending on how long the young remain pelagic, current regimes are such that the spawning areas that produce young *P. octonemus* of the northwestern Gulf can lie almost anywhere in the western or central Gulf. Recent studies (Parker et al. 1979) cited in Rezak et al. (1983) found almost all surface drifters released west of a line from the Mississippi delta to the middle of the Yucatan Straits washed ashore along Texas; those released to the east were almost all found outside the Gulf along the Atlantic coast of Florida. This probably reflects a well-documented picture of Gulf circulation (Nowlin and McLellan 1967, Nowlin 1972, Behringer et al. 1977, Merrell and Morrison 1981, Merrell and Vasquez 1983): The major driving force for nearsurface circulation in the deep eastern Gulf is the Loop Current which enters the Gulf via the Yucatan Straits, loops toward Alabama, and turns back to exit the Gulf via the Florida Straits. The major driving force in the western Gulf is a large, permanent anticyclonic gyre, centered at 23.5°N, and maintained by consistent pinching off and westward drift of Loop Current rings (Merrell and Morrison 1981) or wind stress curl across the western Gulf (Sturges and Blaha 1976, Merrell and Vasquez 1983). South of this gyre is a cyclonic gyre in the Bay of Campeche from which water joins a predominantly northerly flow along the Mexican shelf (Nowlin 1972, Merrell and Morrison 1981, Rezak et al. 1983). Pelagic early stages of *P. octonemus* have been collected along much of the western Gulf margin (Fig. 13). The northerly flow there could transport pelagic

young towards Texas. The coastal area off south Texas and northern Mexico has converging currents much of the year, water which at least in part heads easterly or northerly along the shelf edge after leaving the coast near 26°N. Whatever their source, pelagic young transported to and entrained in the gyre of the Texas–western Louisiana shelf could be transported to inshore and estuarine nurseries there.

## Bathymetric distribution, recruitment, and movements

Our finding that *P. octonemus* is most abundant at depths ≤22 m in the northwestern Gulf agrees with Hildebrand (1954) and Chittenden and McEachran (1976), who only captured it in the demersal phase and considered it a member of the white shrimp community. Maximum depths recorded for the demersal form of this species in the Gulf are 66 m off Louisiana (Springer and Bullis 1956) and 65 m off Texas (Wohlschlag et al. 1979).

Our finding that *P. octonemus* appears late March–April and basically disappears late October–late December agrees with the literature for Texas and Louisiana including Gunter (1938b, 1945), Perret et al. (1971), and Gallaway and Strawn (1974). Some reports indicate a few fish occur in winter in the white and brown shrimp communities throughout the northern Gulf: (1) in January in Galveston Bay, Texas (Gallaway and Strawn 1974, Sheridan 1983), (2) at 18–22 m in January off Texas (Chittenden and McEachran 1976), (3) in shallow waters in January and February at Sabine Lake and Holly Beach, Louisiana (Perry and Carter 1979), and (4) at 40 m in early February off Alabama (Bullis and Thompson 1965). The similar periodicity of reported occurrence suggests similar movements and spawning periodicity throughout the northwestern and north-central Gulf.

The spring recruitment we found in *P. octonemus* agrees with data in several studies from the northern Gulf including Gunter (1945) and Miller (1965) in Texas, Gunter (1938b) and Perret et al. (1971) in Louisiana, and Ogren and Brusher (1977) in northwestern Florida. Recruitment appears concurrent in estuaries and the shallow Gulf, because we collected fish 50–105 mm in the Gulf off Texas at ≤9 m in April, the same period when Gallaway and Strawn (1974) and Landry (1977) collected fish in Galveston Bay 56–97 mm (40–69 mm SL) and 74–101 mm (53–72 mm SL), respectively. Moreover, demersal phase fish first appeared the same month in both Barataria Bay and the shallow Gulf off Louisiana (Gunter 1938b).

Our finding that *P. octonemus* disperse offshore beginning in early summer agrees with the literature. Gunter (1945), Gallaway and Strawn (1974), and Perret et al. (1971) found abundance declined in estuaries in June–August or September, at about the same time (July–September) we found greatest abundance in the Gulf and size gradients from estuaries to offshore. We found the largest, oldest fish in the deeper areas of the white shrimp community or in the transition community (Chittenden et al. 1982) as they dispersed offshore. This pattern has also been suggested for other species of the Gulf white shrimp community such as *Micropogonias undulatus*, *Peprilus burti*, *Cynoscion arenarius*, and *Larimus fasciatus* (White and Chittenden 1977, Murphy 1981, Shlossman and Chittenden 1981, Standard and Chittenden 1984).

## Age determination and growth

Age determination, size at age, and von Bertalanffy parameters have not been previously described for *P. octonemus*. Our calculations for growth are based on sizes at known time scaled to calculated hatching dates to give age. Regression coefficients and $K$ values are the same regardless of hatching date, however, because curves are fitted to the same time dimension between the first and last collections of a cohort.

We determined age in months and years by length-frequency analysis because we had almost 4 years of data from cruises so close in time that modes were easily followed, and only one cohort usually occurred at a given time. As in *Stenotomus caprinus* (Geoghegan and Chittenden 1982) and *Larimus fasciatus* (Standard and Chittenden 1984), modal-group progression analysis can be a superior method of age determination in *P. octonemus* because (1) spawning primarily occurs in one discrete period, (2) growth of large and small fish in a cohort appears uniform because variances were generally constant between cruises, (3) length frequencies are reasonably normally distributed within cohorts, and (4) age need only be determined for 1 or 2 years, ideal conditions for using length frequencies (Lagler 1956, Bagenal and Tesch 1978).

Although it would be desirable to support our aging findings by the more time-consuming analysis of daily otolith increments (Jones 1986), the growth and other parameters we present provide useful upper or lower boundaries for true values (see comments in Methods). We reiterate that our sizes at age and von Bertalanffy parameters are apparent ones; they are affected to an unknown degree by a combination of recruitment, and, especially as the fish approach age I, emigration, gear avoidance, and change from demersal to pelagic behavior. Because of similar problems, Knudsen and Herke (1978) suggested length frequencies should not be used to estimate growth in *Micropogonius undulatus*. We do not agree, however, because the fundamental problem is not the length-frequency method. Rather, it is

how best to draw a random sample in time and space to characterize the population. The time dimension has three major aspects of variation (diel, annual, and monthly or seasonal), as does the spatial (along-shelf, across-shelf and estuary, and vertical). No published Gulf study to our knowledge addressed all six aspects, and few addressed any to the extent we did. Our design directly addressed all three time aspects and the across-shelf spatial dimension. We addressed along-shelf and estuarine variation indirectly by referencing the considerable literature. We were not able to address vertical variation, but apparently no published work has done that. The problem of getting representative data for *P. octonemus*—indeed, for many other Gulf species—may not be fully solved till all six aspects of sampling are concurrently addressed in one study.

## Maximum size, life span, and mortality

The largest *P. octonemus* we collected in the northwestern Gulf (229 mm) is very close to that reported from off Virginia (233 and 235 mm ?L, Hildebrand and Schroeder 1928), the only Atlantic coast location with published sizes. Breder (1948) noted this species reaches one foot in length but gave no details to support the figure; it is only 2–3 inches larger than our maximum sizes and might reflect a rough rounding-off by him. The largest *P. octonemus* we found is slightly larger than maximum sizes in other Gulf studies [off Texas: 213 mm (Gunter 1945), 210 mm (Compton and Bradley 1963), 213 mm (171 mm FL) (Chittenden and McEachran 1976); Off Mississippi: 197 mm (Christmas and Waller 1973); Off Florida: 209 mm ?L (Powell et al. 1972)]. However, these reported maximum lengths are similar to the apparent typical maximum size of 202–206 mm we found. Smaller maximum sizes in other Gulf reports such as Gunter (1938b), Perret et al. (1971), Gallaway and Strawn (1974), and Perry and Carter (1979) may reflect gear selectivity or the fact they collected largely in estuaries, surf, and shallow Gulf areas. The studies cited, however, took place over much of the northern Gulf so the demersal stage of *P. octonemus* appears to show little, if any, east-west spatial variation in maximum sizes.

Our finding the largest, oldest *P. octonemus* in the deeper areas of the white shrimp community may reflect a broad life-history pattern for species there, many of which show a positive size gradient towards offshore. This has been reported for strongly estuarine dependent species such as *Micropogonius undulatus* and *Cynoscion arenarius* (White and Chittenden 1977, Shlossman and Chittenden 1981), and more marine forms such as *Peprilus burti* and *Larimus fasciatus* (Murphy 1981, Standard and Chittenden 1984).

The apparent typical maximum life span of 1 year we found for *P. octonemus* in the northwestern Gulf agrees with Chittenden and McEachran (1976) and appears reasonable, at least for the demersal stage, because the maximum and typical maximum sizes we observed are similar to, or larger than, all other values reported for the Gulf. The value of $t_L = 1$ year might be a little low because *P. octonemus* disappears at 9–11 months of age to spawn in winter, and because we collected one fish 15 months of age in April. That one fish is the only instance in 71 cruises in which a second year class co-occurred with young-of-the-year, so our data clearly indicate that at least the demersal phase of life basically ends at 1 year. Though the literature indicates no east-west spatial variation in maximum size, and age by inference, *P. octonemus* might survive their first spawning and assume a pelagic behavior. Bullis (1961) observed a dense ball of small *Polydactylus* sp., which could have been young or adult *P. octonemus*, *P. virginicus*, or *P. oligodon* (Fischer 1978), at the surface along the 500-fm curve in August in the western Caribbean.

Midwater and surface collections are needed to resolve the duration of a pelagic phase in adult *P. octonemus*; that would clarify the validity of the several life-history parameter values we have termed "apparent." In addition, collections with trawls larger than we and other workers have used would clarify if and how gear-avoidance affects parameter values. Despite these possible problems, however, it seems clear that few adult *P. octonemus* resume a demersal existence in the white or brown shrimp communities after age I. We collected only one fish older than 12 months, and Chittenden and McEachran (1976) caught no fish older than 12 months even though they caught 33 specimens on the white shrimp grounds in January.

The apparent mean time- and cohort-specific total annual mortality rates we observed for *P. octonemus* (97–100%) agree with theoretical estimates of 90–100% (Royce 1972:238) if maximum life span is typically only 1–2 years. Though these are also apparent values, they are not that far from the range of values for another well-studied, exploited pelagic species, *Brevoortia patronus*. In that species, total annual mortality rate is 83–95% depending on age (Nelson and Ahrenholz 1986). Moreover, the population dynamics of *P. octonemus* in the northwestern Gulf appear generally similar to those reported for many other species there including *Micropogonius undulatus* (White and Chittenden 1977), *Cynoscion arenarius* (Shlossman and Chittenden 1981), *Cynoscion nothus* (DeVries and Chittenden 1982), *Peprilus burti* (Murphy 1981), *Stenotomus caprinus* (Geoghegan and Chittenden 1982), *Larimus fasciatus* (Standard and Chittenden 1984), and *Leiostomus xanthurus* (Hata 1985). This similar-

ity over a variety of species supports the suggestions (Chittenden and McEachran 1976, Chittenden 1977) that fishes of the white and brown shrimp communities, at least in the northwestern Gulf, have evolved a common pattern of population dynamics which stresses small size, early maturity, short life spans, high mortality rates, and rapid turnover of biomass.

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**Abstract.**—The feeding habits of late-larval and early-juvenile walleye pollock *Theragra chalcogramma* from a coastal nursery habitat in the western Gulf of Alaska were examined in relation to fish size (10.0–29.9 mm SL) and site of collection. *Pseudocalanus* sp. was the dominant prey. Copepod nauplii and *Pseudocalanus* copepodids decreased in importance in the diet as fish size increased, concomitant with an increase in importance of adult *Pseudocalanus* sp. and *Calanus* spp. Other prey showed no clear relation to fish size. A comparison of diet between collection stations revealed considerable variability. Along two transects perpendicular to the Alaska Peninsula, between-station diet overlap was observed to be high for one transect, and low for the other. Along a transect parallel to the Alaska Peninsula, some adjacent stations yielded high diet overlap, and other yielded low overlap, while the most distant stations produced high diet overlap. Patchiness of food resources likely contributed subtantially to these patterns. One possible consequence of the ingestion of different prey in different locales is that differential growth rates could result.

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# Feeding Ecology of Late-Larval and Early-Juvenile Walleye Pollock *Theragra chalcogramma* from the Gulf of Alaska in 1987*

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The recent discovery of large spawning aggregations of walleye pollock *Theragra chalcogramma* in Shelikof Strait from late March to mid-April suggests that this is the principal spawning center for the species in the Gulf of Alaska (Dunn et al. 1984, Kendall et al. 1987). The concentrated mass of eggs produced in Shelikof Strait in early spring and the ensuing dense patch of larvae provide uncommon access to the early life history of the species. The spawning aggregations produce distinct cohort patches (20 × 50 km or larger) of eggs at depths greater than 150 m (Incze et al. 1989). After about 14 days, the eggs hatch (Dunn and Matarese 1987, Kim 1989) and larvae ascend to the upper 50 m (Incze et al. 1989). The larval patches can be followed for up to 30 days as they drift with prevailing currents to the southwest (Kendall et al. 1987, Hinckley et al. 1989, Incze et al. 1989). The cohesiveness of the patches likely results from the restricted spawning area within Shelikof Strait (Hinckley et al. 1989) as well as Alaska Coastal Current circulation patterns (Incze et al. 1989).

Ichthyoplankton has been surveyed regularly in and around Shelikof Strait since 1979, and much is known regarding the early life history of walleye pollock in this area (e.g., Kendall et all 1987, Incze et al. 1989, Kim 1989, Yoklavich and Bailey 1989). However, considerably less is known about life history of late-larval and juvenile stages within nursery habitats in the western Gulf of Alaska. A survey in June and July 1987 collected late-larval and early-juvenile pollock from a coastal nursery area over the continental shelf along the Alaska Peninsula (Hinckley et al. 1989). While the center of distribution was between the Shumagin and Semidi Islands, a large number of late larvae and juveniles were collected over a broad area running nearly the length of the Alaska Peninsula. The broad distribution enabled us to examine whether diet varied along the length of the Alaska Peninsula and along a nearshore-offshore transect. Although the feeding habits of the late larvae have been previously reported from several locations, in all cases results have been pooled across collection stations (Kamba 1977, Clarke 1978, Cooney et al. 1980, Lee 1985, Kendall et al. 1987). In the present study, feeding habits of late larvae were analyzed by size and these data are compared to previous reports. Further, diet was analyzed by collection station, and between-station differences were examined using a measure of diet overlap.

## Materials and methods

Pollock larvae were collected in the Gulf of Alaska during June 1987 by the RV *Miller Freeman*. Collections were made using a 5-$m^2$ Methot frame trawl (Methot 1986) (2 × 3 mm oval mesh) that was fished obliquely

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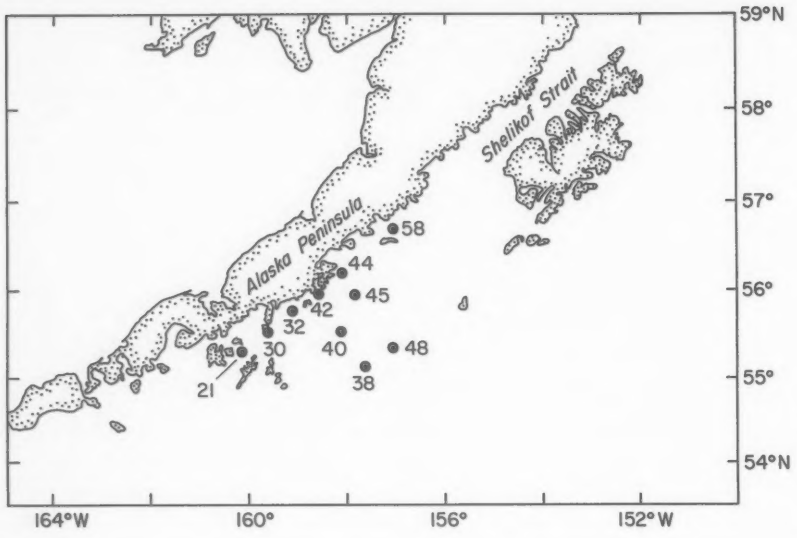


**Figure 1**
Location of collection stations in the Gulf of Alaska. Stations represent one transect parallel to the Alaska peninsula, and two perpendicular offshore transects, with stations 38 and 48 located near the shelf break.

from 15 m off-bottom (to a maximum of 300 m depth) to the surface (Hinckley et al. 1989). Samples from 10 stations, representing 2 nearshore-offshire transects (stations 38, 40, and 42 and stations 44, 45, and 48) and one transect parallel to the Alaska Peninsula (stations 21, 30, 32, 42, 44, and 58; see Figure 1), that were collected from 20 to 25 June, were the focus of this study. The total number of fish examined was 490.

Samples were preserved in 5% formalin at sea, and transferred to 70% ethanol prior to their examination. Specimen shrinkage most likely occurred as a result of fixation.

After the standard length (SL) of each larva was measured, the digestive tract was removed. Contents of the entire digestive tract were evaluated. Gut contents were teased out and prey items were identified: invertebrate eggs, copepod nauplii, barnacle nauplii, euphausiid larvae, pteropods, other non-copepod prey, and copepods including *Pseudocalanus* sp. adults (CVI), *Pseudocalanus* copepodids (CI–CV), *Acartia longiremis*, *Acartia* sp., *Calanus marshallae*, *Calanus* sp., *Centropages abdominalis*, *Eucalanus bungii*, *Metridia* sp., *Oithona* sp., *Oncaea* sp., unidentified calanoid copepodids <1.5 mm, and unidentified calanoid copepodids >1.5 mm. Copepod eggs comprised over 99% of the "invertebrate eggs" category and *Oithona similis* comprised over 99% of the "*Oithona* sp." category. While the taxonomy of the genus *Pseudocalanus* has recently been clarified (Frost 1989), no attempt at specific identifications of *Pseudocalanus* was made in the present study. For all copepods except *Pseudocalanus* sp., copepodid (CI–CV) through adult stages were considered together. Copepodids were inconsequential in all species except *Calanus* sp.

Diet was analyzed in terms of numerical percentage composition (%$N$), volumetric percentage composition (%$VOL$), and percent frequency of occurrence (%$FO$). Prey volumes were estimated using prey dimensions (Grover and Olla 1987). Over 8000 prey items were measured for prey volume calculations. The three analyses (%$N$, %$VOL$, and %$FO$) were combined to yield a more comprehensive assessment of prey importance, the index of relative importance ($IRI = (\%N + \%VOL) \times \%FO$) (Pinkas et al. 1971). Data were pooled across stations for analysis by size class. The four size classes were defined as 10.0–14.9, 15.0–19.9, 20.0–24.9, and 25.0–29.9 mm SL. For station-by-station analyses, data were pooled across size classes.

Diet overlap was calculated using an index of proportional similarity (Wallace 1981, Linton et al. 1981, Kohn and Riggs 1982) defined as

$$PS = 1 - 0.5\left(\sum_{i=1}^{n} \left|P_{xi} - P_{yi}\right|\right)$$

where $PS$ is the index of proportional similarity or overlap, $P_{xi}$ is the proportion of prey category $i$ in the diet at location $x$, $P_{yi}$ is the proportion of prey category $i$ in the diet at location $y$, and $n$ is the number of prey categories. Mean percent volume was used as a measure of diet for these calculations (Wallace 1981). Although this index has been traditionally used to examine diet overlap between species at one location, I have used it to examine diet overlap between locations for

**Table 1**
Mean lengths of late-larval and early-juvenile walleye pollock collected at 10 stations in the Gulf of Alaska in 1987 (with standard deviations), and date and time of collection.

| Station no. | Standard length (mm) | Collection Date | Collection Time (h) |
|---|---|---|---|
| 21 | 16.1 (2.11) | 20 June | 2156 |
| 30 | 18.2 (2.27) | 22 June | 0144 |
| 32 | 17.4 (1.74) | 22 June | 0704 |
| 38 | 19.3 (3.27) | 22 June | 2205 |
| 40 | 18.6 (2.06) | 23 June | 0114 |
| 42 | 18.4 (2.44) | 23 June | 0558 |
| 44 | 17.1 (2.47) | 24 June | 1756 |
| 45 | 19.9 (2.40) | 24 June | 1956 |
| 48 | 20.2 (2.55) | 25 June | 0117 |
| 58 | 19.0 (3.36) | 25 June | 2314 |

a single species. This index was chosen because it does not require resource-availability data (Wallace 1981), it is independent of sample size (Kohn and Riggs 1982), and it estimates overlap accurately for real overlaps between 7 and 85%, whereas three other indices performed poorly (Linton et al. 1981). *PS* values greater than 60% are generally considered to demonstrate significant overlap (Mathur 1977, Wallace and Ramsey 1983). In order to minimize size-related bias in the measurement of diet overlap, proportional similarity indices were calculated for only the 15.0–19.9 mm SL size class.

## Results

Standard length tended to increase with date of collection (Table 1, correlation coefficient $r = 0.678$, $P < 0.05$). The dominant size class for all stations was 15.0–19.9 mm SL, accounting for 62% of the larvae, with a minimum of 21 larvae of this size collected at each station. The mean lengths of larvae from five stations located along a transect parallel to the Alaska Peninsula were significantly different ($P<0.001$) (ANOVA, Zar 1974), while of the two transects perpendicular to the Alaska Peninsula, larval lengths were significantly different ($P<0.001$) along only one of these transects (stations 44, 45, and 48).

**Table 2**
Diet of walleye pollock from the Gulf of Alaska in 1987, by size class, expressed as %*N*, %*VOL*, %*FO*, and %*IRI*.

| | 10.0–14.9 mm SL (*N*=50) | | | | 15.0–19.9 mm SL (*N*=302) | | | | 20.0–24.9 mm SL (*N*=127) | | | | 25.0–29.9 mm SL (*N*=7) | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | %*N* | %*VOL* | %*FO* | %*IRI* | %*N* | %*VOL* | %*FO* | %*IRI* | %*N* | %*VOL* | %*FO* | %*IRI* | %*N* | %*VOL* | %*FO* | %*IRI* |
| Invertebrate eggs | 15.8 | 0.8 | 66.0 | 7.3 | 25.8 | 0.9 | 62.6 | 12.4 | 27.1 | 0.6 | 67.7 | 13.3 | 15.9 | 0.3 | 42.9 | 4.7 |
| Copepod nauplii | 25.3 | 2.8 | 86.0 | 16.1 | 9.3 | 0.7 | 63.2 | 4.7 | 1.5 | 0.1 | 40.9 | 0.5 | 0.5 | <0.1 | 14.3 | <0.1 |
| Barnacle nauplii | | | | | 0.1 | <0.1 | 4.3 | <0.1 | 0.1 | <0.1 | 4.7 | <0.1 | | | | |
| Euphausiids | 1.1 | 6.4 | 24.0 | 1.2 | 0.8 | 3.0 | 20.5 | 0.6 | 0.7 | 1.9 | 20.5 | 0.4 | 0.7 | 1.3 | 28.6 | 0.4 |
| Pteropods | 0.6 | 0.3 | 8.0 | <0.1 | 1.6 | 0.5 | 16.9 | 0.3 | 0.4 | 0.1 | 6.3 | <0.1 | | | | |
| Other | | | | | 0.2 | 0.1 | 5.3 | <0.1 | <0.1 | <0.1 | 3.1 | <0.1 | | | | |
| *Pseudocalanus* sp. | 8.8 | 30.7 | 82.0 | 21.6 | 14.6 | 35.5 | 79.5 | 29.5 | 26.6 | 43.1 | 87.4 | 43.3 | 37.2 | 40.7 | 100.0 | 52.9 |
| *Pseudocalanus* copepodids | 6.7 | 9.1 | 76.0 | 8.0 | 7.5 | 7.2 | 66.6 | 7.3 | 7.8 | 5.0 | 69.3 | 6.3 | 8.6 | 3.7 | 57.1 | 4.8 |
| *Acartia longiremis* | 6.4 | 13.8 | 64.0 | 8.6 | 9.2 | 14.0 | 66.2 | 11.4 | 6.9 | 7.0 | 69.3 | 6.8 | 2.1 | 1.4 | 42.9 | 1.0 |
| *Acartia* sp. | 1.0 | 1.5 | 22.0 | 0.4 | 0.9 | 1.0 | 18.2 | 0.2 | 0.6 | 0.4 | 11.0 | 0.1 | | | | |
| *Calanus marshallae* | <0.1 | 0.9 | 2.0 | <0.1 | 0.3 | 3.5 | 10.3 | 0.3 | 0.9 | 7.2 | 27.6 | 1.6 | 3.2 | 18.3 | 57.1 | 8.4 |
| *Calanus* sp. | | | | | 0.1 | 2.5 | 5.0 | 0.1 | 0.4 | 4.6 | 11.8 | 0.4 | 0.7 | 5.7 | 14.3 | 0.6 |
| *Centropages abdominalis* | 0.2 | 1.3 | 6.0 | <0.1 | 0.2 | 0.9 | 8.9 | 0.1 | 0.3 | 0.8 | 14.2 | 0.1 | | | | |
| *Eucalanus bungii* | | | | | 0.2 | 6.5 | 5.0 | 0.2 | 0.6 | 11.3 | 15.0 | 1.2 | 0.9 | 12.3 | 14.3 | 1.3 |
| *Metridia* sp. | <0.1 | 0.9 | 2.0 | <0.1 | <0.1 | 0.4 | 1.3 | <0.1 | | | | | | | | |
| Unident. copepodids <1.5 mm | 14.4 | 20.3 | 96.0 | 22.1 | 15.5 | 15.3 | 95.7 | 21.8 | 17.6 | 11.6 | 95.3 | 19.8 | 19.4 | 8.6 | 85.7 | 16.3 |
| Unident. copepodids >1.5 mm | <0.1 | 0.6 | 2.0 | <0.1 | 0.4 | 2.9 | 12.3 | 0.3 | 0.8 | 4.3 | 24.4 | 0.9 | 1.6 | 6.1 | 42.9 | 2.2 |
| *Oithona* sp. | 18.5 | 10.2 | 76.0 | 14.5 | 12.9 | 4.9 | 80.8 | 10.7 | 7.6 | 1.9 | 76.4 | 5.2 | 9.2 | 1.6 | 100.0 | 7.4 |
| *Oncaea* sp. | 1.0 | 0.4 | 18.0 | 0.1 | 0.3 | 0.1 | 7.3 | <0.1 | 0.1 | <0.1 | 2.4 | <0.1 | | | | |

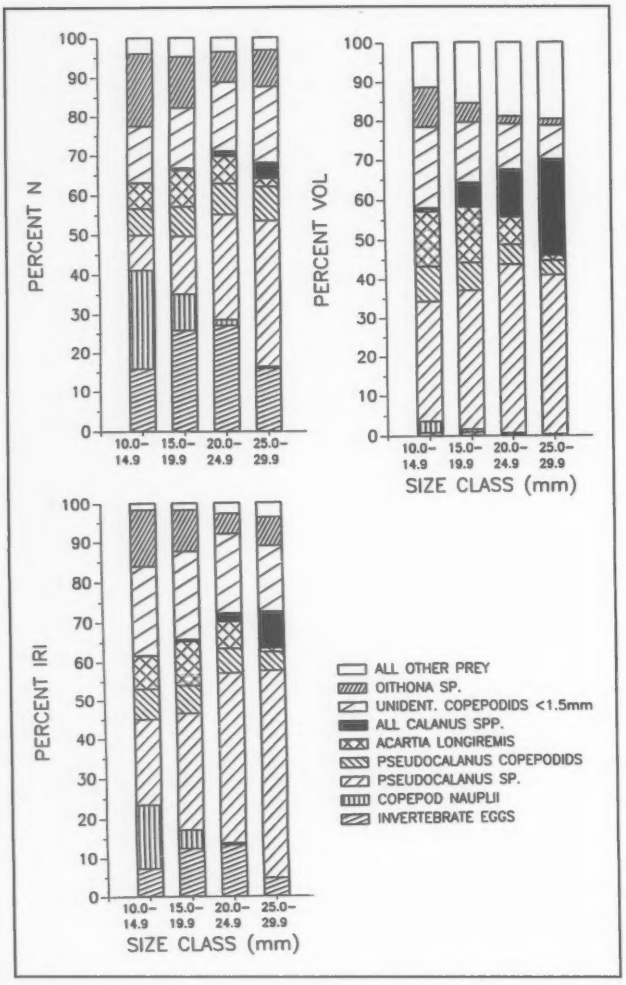


**Figure 2**
The diet of larval pollock in the Gulf of Alaska in June 1987, by size class, in terms of *%N*, *%VOL*, and *%IRI*.

## Diet as a function of size

Small unidentified calanoid copepodids (i.e., <1.5 mm) were the primary prey (*IRI*) for larvae 10.0–14.9 mm SL, followed by *Pseudocalanus* sp. (Table 2, Fig. 2). Copepod nauplii, which ranked as a major food item for only this size class, was third in importance, followed by *Oithona* sp. and *Acartia longiremis*.

For larvae 15.0–19.9 mm SL, the same two prey items dominated the diet, but *Pseudocalanus* sp. was the most important item and small (unidentified) calanoid copepodids were second (Table 2, Fig. 2). Invertebrate eggs, *A. longiremis*, and *Oithona* sp. ranked third through fifth.

For fish 20.0–24.9 mm SL, *Pseudocalanus* sp. contributed twofold more to the diet than any other item (Table 2, Fig. 2). Small calanoid copepodids, invertebrate eggs, and *A. longiremis* were second, third, and fourth most important prey, followed by *Pseudocalanus* copepodids.

*Pseudocalanus* sp. continued to be the dominant prey for the largest size class that was examined, 25.0–29.9 mm SL, comprising over 52% of the diet, with small calanoid copepodids ranking second in importance (Table 2, Fig. 2). These were followed by *Calanus marshallae*, a species whose only major contribution to the diet was in this size class, *Oithona* sp., and *Pseudocalanus* copepodids.

Considering adult and copepodid forms together, *Pseudocalanus* sp. was the principal prey for all sizes of larvae and early juveniles (Table 2, Fig. 2). The contribution of *Pseudocalanus* sp. adults and all *Calanus* spp. increased directly in relation to fish size. On the

**Table 3**
Diet of larval walleye pollock in the Gulf of Alaska in 1987, by station, expressed as %*IRI*.

| | Station number | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 21 | 30 | 32 | 38 | 40 | 42 | 44 | 45 | 48 | 58 |
| Invertebrate eggs | 6.5 | 0.3 | 16.7 | 12.4 | 1.4 | 28.3 | 13.3 | 26.1 | 6.9 | 0.2 |
| Copepod nauplii | 9.9 | 5.5 | 9.1 | 0.6 | 0.6 | 1.2 | 1.3 | 0.6 | 0.7 | 10.2 |
| Barnacle nauplii | | <0.1 | 0.1 | | | <0.1 | 0.1 | | | <0.1 |
| Euphausiids | 5.2 | 0.4 | 0.7 | 1.2 | 0.5 | 0.2 | 0.7 | <0.1 | <0.1 | <0.1 |
| Pteropods | | | 10.7 | | 0.9 | <0.1 | <0.1 | <0.1 | | |
| Other | <0.1 | | 0.4 | <0.1 | <0.1 | | <0.1 | | | <0.1 |
| *Pseudocalanus* sp. | 23.3 | 4.5 | 7.4 | 32.8 | 5.2 | 31.4 | 39.2 | 50.0 | 49.1 | 41.2 |
| *Pseudocalanus* copepodids | 11.3 | 0.1 | 2.8 | 13.2 | 0.3 | 5.3 | 11.1 | 7.1 | 4.6 | 6.0 |
| *Acartia longiremis* | 1.7 | 22.2 | 7.9 | 5.6 | 53.7 | 4.5 | 5.8 | 1.0 | 6.1 | 11.2 |
| *Acartia* sp. | 0.1 | 0.2 | 5.1 | <0.1 | | 3.6 | <0.1 | | | <0.1 |
| *Calanus marshallae* | | 0.5 | | 7.0 | 0.2 | <0.1 | 0.7 | 0.1 | 0.4 | 0.5 |
| *Calanus* sp. | <0.1 | | 0.1 | | <0.1 | | | 0.2 | 6.6 | |
| *Centropages abdominalis* | <0.1 | 0.1 | 0.3 | <0.1 | 0.1 | 0.2 | <0.1 | | 0.4 | <0.1 |
| *Eucalanus bungii* | | | | 3.1 | 13.5 | | | | | |
| *Metridia* sp. | <0.1 | <0.1 | | | | | <0.1 | <0.1 | | |
| Unident. copepodids <1.5 mm | 16.1 | 37.8 | 15.7 | 16.7 | 17.2 | 22.7 | 23.3 | 13.2 | 21.7 | 20.1 |
| Unident. copepodids >1.5 mm | <0.1 | 21.1 | | 0.8 | 0.7 | <0.1 | <0.1 | <0.1 | 0.4 | 0.1 |
| *Oithona* sp. | 25.7 | 7.2 | 22.7 | 6.5 | 5.6 | 2.4 | 4.4 | 1.6 | 3.1 | 10.4 |
| *Oncaea* sp. | 0.1 | | 0.3 | <0.1 | | 0.1 | <0.1 | <0.1 | | <0.1 |

other hand, the contribution of *Pseudocalanus* copepodids and copepod nauplii decreased with increasing fish size. Other major prey categories (i.e., small calanoid copepodids, invertebrate eggs, *A. longiremis*, and *Oithona* sp.) showed no clear relation to fish size.

## Diet as related to site of collection

*Pseudocalanus* sp. was the most important prey at 6 of the 10 stations, accounting for over 30% (*IRI*) of the diet at each of these locations (Table 3, Fig. 3). Small calanoid copepodids were of secondary importance, ranging from 13.2 to 23.3%, while invertebrate eggs, copepod nauplii, *Pseudocalanus* copepodids, and *A. longiremis* and *Oithona* sp. each contributed more than 10% to the diet at one or more of these stations.

At two of the remaining four stations *Oithona* sp. was the primary prey (22.7–25.7%). Small calanoid copepodids were most important at another staion (37.8%), and *A. longiremis* was dominant at the remaining one, comprising more than 53% of the diet. Additionally, invertebrate (mostly copepod) eggs, copepod nauplii, pteropods, *Pseudocalanus* sp., *Pseudocalanus* copepodids, *A. longiremis*, *Eucalanus bungii*, and small and large unidentified calanoid copepodids (i.e., >1.5 mm), were well represented in the diet at one or more of the stations that were not dominated by *Pseudocalanus* sp.

## Diet overlap between stations

Values of the index of proportional similarity (*PS*) varied widely, franging from 0.252 to 0.833 (Table 4). Of 11 pairs of adjacent stations, 45% showed no significant diet overlap, while of 34 pairs of non-adjacent stations 50% showed no significant overlap. Two stations, 30 and 40, were quite dissimilar from all other stations, and station 32 showed significant overlap only in relation to stations 21 and 58.

When examining diet overlap for the six stations that comprise the transect parallel to the Alaska Peninsula, a high degree of variation was seen in *PS* values (Table 5). At the southwestern end of the transect the lowest *PS* value was obtained for stations in closest proximity (21 and 30), while at the northeastern end of the transect the greatest *PS* value was obtained for stations in closest proximity (58 and 44). At the same time, diet at the two most distanct stations (21 and 58) showed great similarity.

Along one of the two transects perpendicular to the Alaska Peninsula (stations 44, 45, and 48), *PS* values indicated considerable overlap (Table 6). In contrast, a different pattern was obtained along the other perpendicular transect (stations 38, 40, and 42) where *PS* values were wide-ranging. For each of the two transects the greatest diet overlap was between the nearshore and offshore extremes of the transect (i.e., stations 44 and 48, and stations 38 and 42).

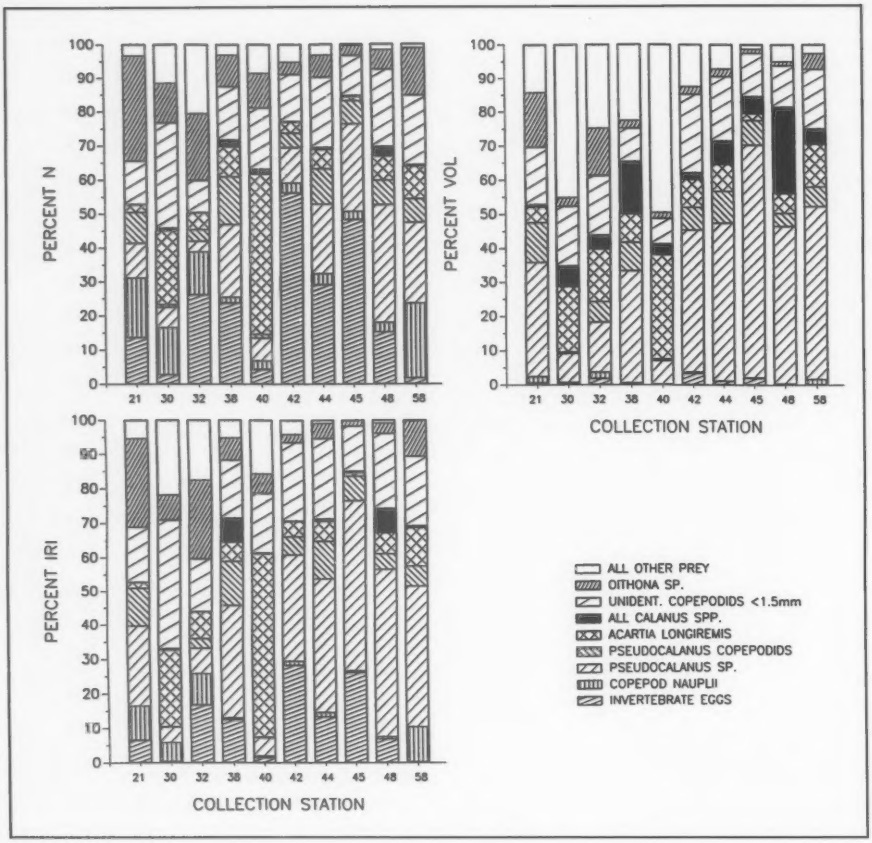


**Figure 3**
The diet of larval pollock in the Gulf of Alaska in June 1987, by collection station in terms of %*N*, %*VOL*, and %*IRI*.

**Table 4**
Index of proportional similarity (*PS*) for walleye pollock 15.0–19.9 mm SL, at all stations, calculated using mean volume data. *PS* values for adjacent stations are underlined.

| Sta. no. | 21 | 30 | 32 | 38 | 40 | 42 | 44 | 45 | 48 | 58 |
|---|---|---|---|---|---|---|---|---|---|---|
| 21 | * | | | | | | | | | |
| 30 | 0.384 | * | | | | | | | | |
| 32 | 0.605 | 0.504 | * | | | | | | | |
| 38 | 0.652 | 0.475 | 0.507 | * | | | | | | |
| 40 | 0.303 | 0.577 | 0.433 | 0.519 | * | | | | | |
| 42 | 0.695 | 0.458 | 0.591 | 0.682 | 0.328 | * | | | | |
| 44 | 0.770 | 0.474 | 0.524 | 0.742 | 0.353 | 0.833 | * | | | |
| 45 | 0.658 | 0.287 | 0.399 | 0.628 | 0.252 | 0.689 | 0.755 | * | | |
| 48 | 0.676 | 0.415 | 0.490 | 0.676 | 0.368 | 0.760 | 0.805 | 0.728 | * | |
| 58 | 0.782 | 0.547 | 0.626 | 0.810 | 0.441 | 0.754 | 0.831 | 0.645 | 0.706 | * |

**Table 5**
Index of proportional similarity (*PS*) for walleye pollock 15.0–19.9 mm SL, along transect parallel to the Alaska Peninsula, calculated using mean volume data. *PS* values for adjacent stations are underlined.

| Sta. no. | 21 | 30 | 32 | 42 | 44 | 58 |
|---|---|---|---|---|---|---|
| 21 | * | | | | | |
| 30 | 0.384 | * | | | | |
| 32 | 0.605 | 0.504 | * | | | |
| 42 | 0.695 | 0.458 | 0.591 | * | | |
| 44 | 0.770 | 0.474 | 0.524 | 0.833 | * | |
| 58 | 0.782 | 0.547 | 0.626 | 0.754 | 0.831 | * |

**Table 6**
Index of proportional similarity (*PS*) for walleye pollock, 15.0–19.9 mm SL, along two transects perpendicular to the Alaska Peninsula, calculated using mean volume data. *PS* values for adjacent stations are underlined.

| Sta. no. | 38 | 40 | 42 |
|---|---|---|---|
| 38 | * | | |
| 40 | 0.519 | * | |
| 42 | 0.682 | 0.328 | * |
| | 44 | 45 | 48 |
| 44 | * | | |
| 45 | 0.755 | * | |
| 48 | 0.805 | 0.728 | * |

## Discussion

The portion of the present study dealing with the relationship between diet and fish size complements the study by Kendall et al. (1987) conducted in the Gulf of Alaska during May 1983. As the samples in 1983 were collected earlier in the year using different gear (a 505-μm mesh bongo net) than in 1987, the size range of larvae was substantially different in the two studies. However, a comparison of the diet of larvae 10.0–19.0 mm can be made between the two years. From this it was clear that copepod eggs and nauplii were of some consequence in the diet in both years. A between-year comparison of the relative importance of *Pseudocalanus* sp. adults and copepodids cannot be made because the 1983 dietary analysis considered adult and immature stages together as copepodids (CI–CVI). In both years *Pseudocalanus* sp. was the dominant copepod, followed by *Acartia* sp. and *Oithona* sp. As *Pseudocalanus* sp. carries its eggs (Corkett and McLaren 1978), the majority of copepod eggs in the diet were probably incidentally ingested attached to adult females. However, berried females were not observed in pollock stomachs. While the delicate structure of *Pseudocalanus* egg sacs may preclude larval fish from ingesting females with eggs intact (A.J. Paul, Univ Alaska, Seward, pers. commun., Nov. 1988), it is also possible that some of the eggs that were ingested could have been from other genera such as *Acartia* or *Calanus* that broadcast their eggs into the sea (C.B. Miller, Oregon State Univ., Corvallis, pers. commun., June 1989). The source of copepod eggs cannot be resolved without observing female copepods with eggs in the diet or identifying eggs to species. Neither condition was met in the present study.

The dietary importance of copepod nauplii decreased and *Pseudocalanus minutus* increased with increasing larval size for larvae 9–20 mm SL in Uchiura Bay, Hokkaido (Kamba 1977), as was the case in the present study. However, while *A. longiremis*, *Oithona* sp., and various copepodids were important in the Gulf of Alaska, they were not in Uchiura Bay. Since copepod eggs were excluded from the dietary analyses by Kamba, it is not possible to compare their relative importance in Uchiura Bay with the Gulf of Alaska. In the Bering Sea, Clarke (1978) reported that copepod nauplii and *Oithona similis* were the primary prey for pollock 9–18 mm SL, and Cooney et al. (1980) reported that copepodids (CI–CVI) and copepod nauplii were dominant. *Oithona similis* was the dominant copepod species, followed by *Pseudocalanus* sp. and *A. longiremis*. In both Bering Sea accounts, copepod eggs accounted for approximately 5% of the diet of this size class, less than in the Gulf of Alaska.

While the diet of 20.0–29.9 mm SL fish in the Gulf of Alaska appeared to be more diverse than in Uchiura Bay (Kamba 1977), in both areas *Pseudocalanus* sp. was the dominant prey, and *Calanus* sp. was well represented in the diet. In the Bering Sea *Pseudocalanus* sp. copepodids were the dominant prey and copepod eggs were also very important in the diet of early juveniles, although a broader size class, 20.1–60.0 mm SL, was utilized (Cooney et al. 1980). In a more recent study, also in the Bering Sea, cyclopoid copepods proved to be the primary prey for fish 20.0–29.9 mm TL, with *Pseudocalanus* sp. adults second in importance (Lee 1985). In the Gulf of Alaska, *Oithona* sp. (the dominant cyclopoid) was of highly localized importance.

The manner in which diet of larval and juvenile pollock varied between different locales and between years in the same locale illustrates how diet may vary in response to available food resources, which vary in response to oceanographic conditions (e.g., Grover and Olla 1987). As plankton data for the present study were unavailable, the extent to which diet resulted from prey selectivity cannot be determined. However, assuming that diet was at least reflective of available food resources, the wide range in *PS* values would indicate that food resources were not homogeneous. Diet varied widely from station to station, with nearly as many nonadjacent as adjacent station pairs showing significant dietary overlap. This type of variation would suggest areas of planktonic patchiness, perhaps reflecting underlying hydrographic heterogeneities. Low *PS* values may indicate small prey patches, while high values that were seen across several stations may be indicative of large prey patches.

Regardless of whether prey were energetically equivalent at each station, the incidence of feeding was

100%. It is unclear whether differential growth rates may have resulted from the ingestion of different prey since growth rates were not measured in the present study. However, it remains a possibility since Yoklavich and Bailey (1989) reported differential growth rates for late larval and early juveniles at three locations in the Gulf of Alaska in 1987. These fish, which ranged from 12.8 to 40.8 mm SL, were collected in the same survey of late-stage larval pollock (Hinckley et al. 1989) as the present study, from 18 June to 15 July 1987. While specific collection stations differed between the two studies, Yoklavich and Bailey found that growth rates increased from southwest to northeast along the Alaskan Peninsula.

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**Abstract.**–Egg size has been shown to relate to survival and growth in the early life stages of fish. Combined field and laboratory studies examined variation in the egg size of walleye pollock *Theragra chalcogramma*, a commercially important North Pacific gadoid; and a preliminary assessment of the effect of egg size on larval size was made. Differences in egg size were found over parts of the geographical range, among years, and over the spawning season in Shelikof Strait. Egg size did not appear to correlate with female length, age, or condition. Individual female's egg size decreased significantly over the course of the spawning cycle. Preliminary studies in the laboratory showed that egg size is correlated with larval size and may therefore affect mortality in the early larval stages.

# Variation of Egg Size of Walleye Pollock *Theragra chalcogramma* with a Preliminary Examination of the Effect of Egg Size on Larval Size*

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Variability in egg size may be an important factor in the survival of early life stages of fish. It has been proposed by numerous authors (Blaxter and Hempel 1963, Bagenal 1969, Ware 1975, Hunter 1981, Knutsen and Tilseth 1985) that egg size (dry weight or diameter) influences larval survival through its effects on larval size, growth rates, and activity. Larger eggs provide more energy for growth and development (Hempel and Blaxter 1967, Hempel 1979) and generally produce larger larvae which are able to avoid predators more effectively (Miller et al. 1988), survive longer without feeding (Hunter 1981), search a greater volume of water for prey (Blaxter 1986, Webb and Weihs 1986), and eat prey of a greater variety of sizes (Hunter 1981).

Differences in egg size are thought to reflect adaptations by the spawning stock to varying conditions met by early larvae. Bagenal (1971) proposed that there is a relationship among egg size, time of spawning, and availability of food. Cushing (1967) stated that egg size in Atlantic herring *Clupea harengus harengus* is related to the type of production cycle and its variability.

Hunter (1976) indicated that egg size may be important in studies of starvation and predation as cause of larval fish mortality, because of its effects on time to the onset of irreversible starvation, on feeding success, and on the ability of larvae to avoid predators. Larval size and its relation to egg size has been proposed as a unifying factor integrating the dynamics of larval survival and the mechanisms of recruitment. Miller et al. (1988), in their review of this subject, state that "...even small size differences of larvae at hatching can have significant ecological implications, and that even within a species (e.g., herring), size at hatching might be an adaptive response to local geographic conditions."

Walleye pollock *Theragra chalcogramma* is a semidemersal species ranging from Japan around the North Pacific rim to central California. This species supports important commercial fisheries in the Bering Sea and the Gulf of Alaska. Walleye pollock spawn pelagic eggs which have an incubation time of approximately 15 days in 5°C water. Egg diameters have been reported to range from 1.0 to 1.9 mm (Table 1). Larvae are 3–4 mm standard length (SL) at hatching (Dunn and Matarese 1987). Egg size in walleye pollock varies across its geographic range (Table 1). It also varies within populations (Gorbunova 1954, Yusa 1954, Nishiyama and Haryu 1981, Sakurai 1982), and over the course of the spawning season (Serobaba 1968). The causes and significance of egg size variation in walleye pollock are not well known.

This field and laboratory study assesses sources of variation in walleye pollock egg size and presents results of a preliminary study of the relation-

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Fishery Bulletin, U.S. 88:471–483.

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**Table 1**
Geographic variation in walleye pollock egg size.

| Location | Average latitude (°N) | Egg size (mm) Mean | Egg size (mm) Range | Temperature* (°C) (Mean) | Reference |
|---|---|---|---|---|---|
| **Eastern Pacific** | | | | | |
| Puget Sound | 47 | 1.2 | 1.0–1.3 | 8.5 | This study |
| Shelikof Strait | 57 | 1.37 | 1.3–1.4 | 5.0 | This study |
| Bering Sea | 57 | 1.73 | 1.3–1.9 | 3.25 | Nishiyama and Haryu 1981 |
| Bering Sea | 59 | 1.57 | 1.5–1.7 | 0.95 | Serobaba 1968 |
| Bering Sea | 59 | 1.59 | 1.4–1.8 | 2.75 | Serobaba 1974 |
| **Western Pacific** | | | | | |
| Japan | 38 | 1.45 | 1.2–1.7 | 8.0 | Yusa 1954 |
| Peter the Great Bay | 43 | 1.46 | 1.3–1.7 | 2.0 | Gorbunova 1954 |
| S. Kurile Islands | 45 | 1.53 | 1.3–1.8 | 1.43 | Gorbunova 1954 |
| N. Kurile Islands | 48 | 1.61 | 1.4–1.8 | 1.17 | Gorbunova 1954 |
| Sakhalin Island | 50 | 1.58 | 1.5–1.7 | −0.08 | Gorbunova 1954 |
| W. Kamchatka | 56 | 1.57 | 1.3–1.8 | 1.5 | Gorbunova 1954 |

*Temperature at bottom or depth of highest egg abundance (averaged using minimum and maximum of reported range).

ship between egg size and larval size. Size variation in walleye pollock eggs due to annual, seasonal, and geographical factors was examined from eggs caught in ichthyoplankton surveys in the Gulf of Alaska from 1981 to 1986. Variation due to female age, length, and condition was studied using eggs taken from spawning females caught at sea and from females held in the laboratory. Effects of egg size on larval size at hatching and at yolksac absorption were investigated in rearing experiments, using eggs from captive females and eggs taken in ichthyoplankton surveys.

## Methods

### Field studies

Walleye pollock eggs were collected in the Gulf of Alaska between 1981 and 1986 with 60-cm bongo nets (0.505-mm mesh), deployed with standard MARMAP procedures (Posgay and Marak 1980).

Eggs selected for measurement were chosen from archived samples (Table 2) taken in different years (1981–86), months (March–May), and areas (Shelikof Strait, the Semidi Islands to the Shumagin Islands, and west of the Shumagin Islands; Fig. 1). Variation in mean egg size among individual sampling stations was examined by measuring 25–50 eggs from up to 10 stations per year/month/area combination. Eggs at similar stages of development (early blastula to early germ ring) were measured with an ocular micrometer on a dissecting microscope at 40× magnification. All eggs were preserved in 3–5% buffered formalin.

Because mean egg sizes were significantly different ($F = 4.75$, $p<0.0005$) among sampling stations, nested analysis of variance models with unequal cell sizes were used to test year, month, and area effects, with stations as the nested factor. Variation in egg size among years (within area and month), among months (within year and area), and among areas (holding year and month constant) had to be tested separately, due to the incompleteness of the available dataset, including missing months and areas in some years (Table 2).

The General Linear Models procedure of SAS-PC (SAS Inst. 1985) was used in this analysis. The $F$-statistic was derived using the Satterthwaite approximation (Gaylor and Hopper 1969 as cited in Sokal and Rohlf 1981), except in one case where the criteria for using this test were not satisfied; in this case a simple approximation test (Sokal and Rohlf 1981) was used.

Effects of maternal age, size, and condition on egg diameter and dry weight were examined using eggs from females caught by midwater trawl in Shelikof Strait in late March, 1986 (Table 2). Hydrated (fully ripe) eggs were collected from spawning females, and preserved in 5% buffered formalin. For each female, fork length (FL), gonad- and liver-free body weight, and liver weight were determined and otoliths removed for ageing. Body weight and liver weight were used as indices of condition.

Sixty eggs per female were measured. Because hydrated eggs taken from the ovary are sometimes slightly nonspherical, egg diameters were measured on the axis that fell along the transect to make sure measurements were random. Five to ten eggs per fish were subsampled for dry weight; eggs were measured,

**Table 2**

Stratification of walleye pollock egg samples measured for differences in egg size by year, area, and month, and to examine the effect of female size, age, and condition on egg size. Samples were collected on ichthyoplankton cruises in the western Gulf of Alaska.

| | Shelikof Strait | | | Semidi Is. to Shumagin Is. | West of Shumagin Is. |
|---|---|---|---|---|---|
| Year | March | April | May | April | April |
| 1981 | M | Y,M | M | | |
| 1982 | M | Y,A,M | M | A | A |
| 1984 | M | Y,M | M | | |
| 1985 | | Y | | | |
| 1986 | F | Y | | | |

Samples used to study the effect of year (Y), area (A), month (M), and female (F) age, size, and condition.

washed with distilled water, placed individually in preweighed aluminum boats, dried for 24 hours at 60°C, and weighed on a Cahn 29 electrobalance to the nearest 0.001 mg.

An analysis of variance procedure was used to examine egg size within and among fish. A multiple regression model was used to examine the effect of female length, age, and condition on egg diameter and egg weight. The factors in the regression were fork length, age, body weight (minus ovary weight and liver weight), and liver weight. The model used was

$$Y = B_0 + B_1X_1 + B_2X_2 + B_3X_3 + B_4X_4$$

where $Y$ = egg diameter (mm) or egg dry weight (mg),
$X_1$ = fork length (cm),
$X_2$ = age (yr),
$X_3$ = body weight (minus ovary and liver weight, g),
$X_4$ = liver weight (g).

Interaction terms were not included in the model until after a test of the overall significance.

Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

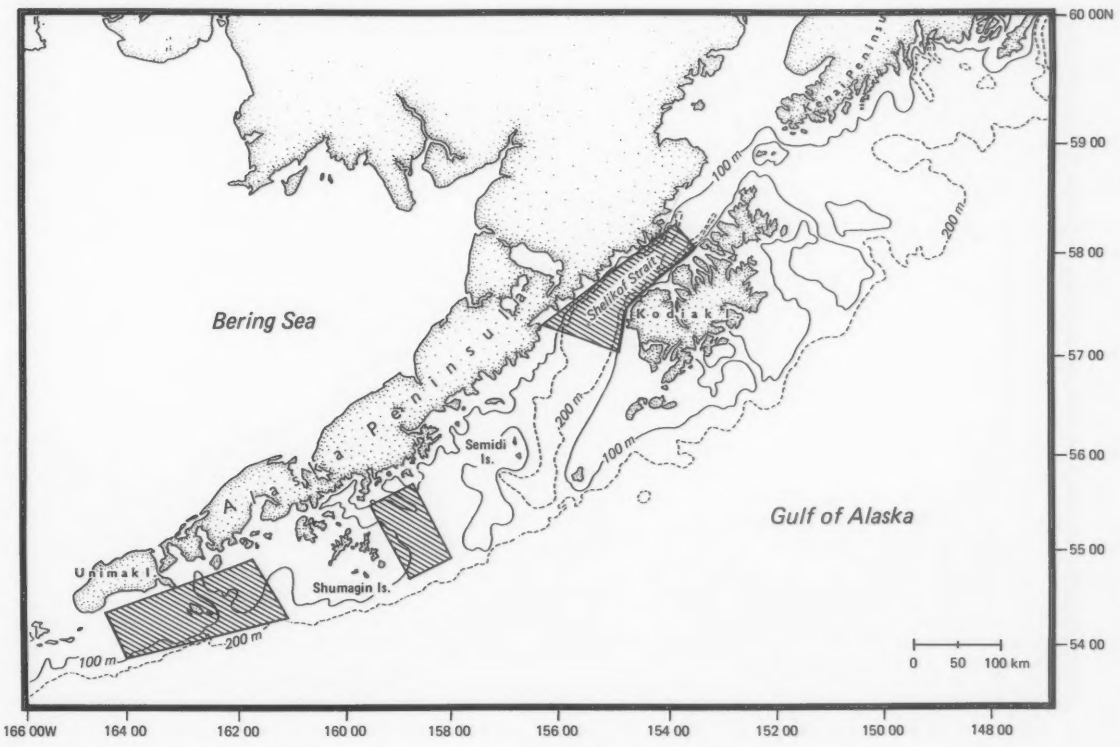


**Figure 1**

Western Gulf of Alaska, including Shelikof Strait, a major spawning area for walleye pollock. Shaded areas indicate regions from which samples were taken.

### Laboratory experiments

Laboratory investigations were conducted using captive walleye pollock in March and April 1987. Adult prespawning walleye pollock were caught in January and February by handline in the Tacoma Narrows region of Puget Sound. Fish were transported to the laboratory and held in net pens under ambient light and temperature conditions and fed chopped herring *ad libidum* until they were nearly in spawning condition (i.e., eggs and milt were expelled with slight pressure to the abdomen). These fish were then transferred to individual 1700- or 2500-L tanks. One female and one or two males were placed in each tank and held throughout their spawning cycle. Water temperatures in the tanks were ambient and varied over the spawning season from 9.5 to 11.5°C ($\bar{x}$ 10.08°C). Ambient water temperature increased significantly ($R^2$=20.9%) over the experimental period. Salinity was constant at 28 ppt. A 20-cm plankton net with a hard codend was suspended in each tank to catch a sample of eggs from each spawning event. Plankton nets were checked each morning for the presence of eggs. If eggs were present in the codend, they were saved, and the water in the tanks replaced.

In 1988, pollock caught in Puget Sound were held individually in tanks to further examine the effect of female length on egg size. Eggs from the first batch from each of seven females were collected and measured in the same manner as described for the 1987 studies.

Egg diameters were measured on 15–25 unpreserved eggs, and egg dry weights were determined for 5–10 eggs from each spawning event. The remainder of the eggs were incubated separately (by female and spawning event) in 4-L jars filled with filtered seawater. The jars were placed in a water bath with running seawater at ambient water temperatures. Light levels were ambient. Water in these jars was changed several times during incubation (which lasted 6–9 days) and dead eggs were removed daily.

Six to fifteen larvae were collected on the day of hatch, anaesthetized with MS222, and their standard lengths measured. The rest of the larvae were held in the 4-L jars until yolksac absorption (defined as the point when individual larvae had used up 90–100% of their yolksacs). Standard lengths were measured (on anaesthetized larvae) and dry weights determined for 5–10 larvae at this stage.

A sample of live eggs collected from the ichthyoplankton in Shelikof Strait was transported to Seattle in April of 1987. Diameters and dry weights were determined on a subsample of these eggs and the rest were incubated. Larvae were measured at hatching and at yolksac absorption in the same manner as described above.

**Table 3**
Differences in mean walleye pollock egg diameter among years in April in the Shelikof Strait region of the Gulf of Alaska.

| Year* | Egg diameter Mean | Egg diameter SE | *N* | SNK grouping** |
|---|---|---|---|---|
| 1981 | 1.360 | 0.003 | 320 | A |
| 1986 | 1.317 | 0.004 | 250 | B |
| 1985 | 1.299 | 0.004 | 250 | C |
| 1984 | 1.298 | 0.003 | 250 | C |
| 1982 | 1.296 | 0.004 | 249 | C |

*Data not available from 1983.
**Student-Newman-Keuls multiple range test (SAS Institute 1985). A, B, C indicate significantly different groups.

Eggs collected from the Gulf of Alaska ichthyoplankton surveys for examination of yearly, seasonal, and regional differences in egg size were preserved in 3–5% formalin. No correction factor was used to correct for changes in egg size due to preservation, as all eggs used in these analyses were preserved in the same manner. The field samples taken from spawning adults and used to examine the relationship between egg size and fish size, age, and condition were also preserved in 3–5% formalin. These, however, were collected before spawning, and the diameters may not be directly comparable to sizes of spawned eggs collected from the ichthyoplankton, due to possible changes in egg size at fertilization and activation (Fleming and Ng 1987, Kjørsvik and Lonning 1983). Eggs from the laboratory were measured fresh and are therefore not directly comparable with eggs from the field studies. The comparison between sizes of Gulf of Alaska eggs and Puget Sound eggs was made only on the fresh samples collected in 1987 from both areas.

## Results

### Geographical, seasonal, and regional differences in egg size

Examination of 1319 walleye pollock eggs from April plankton samples (the month when most spawning occurs; Kim 1987) collected in Shelikof Strait demonstrated a significant difference in mean egg diameters among years ($F$ = 19.862, $p$<0.0005). Mean egg diameter was largest (Table 3) in 1981 and smallest in 1982; there was a 4.7% difference in size between these years. Mean egg size was not statistically different in 1982, 1984, and 1985 (SNK test, Table 3). Mean egg size was intermediate in 1986.

**Table 4**
Differences in mean walleye pollock egg diameter over the spawning season in Shelikof Strait for 1981, 1982, and 1984.

| Year | Month | Egg diameter Mean | SE | *N* | SNK grouping |
|---|---|---|---|---|---|
| 1981 | March | 1.405 | 0.007 | 103 | A |
| | April | 1.360 | 0.003 | 320 | B |
| | May | 1.297 | 0.005 | 204 | C |
| 1982 | March | * | | | |
| | April | 1.296 | 0.004 | 249 | A |
| | May | 1.314 | 0.006 | 159 | B |
| 1984 | March | 1.383 | 0.002 | 792 | A |
| | April | 1.299 | 0.004 | 250 | B |
| | May | * | | | |

*Data not available from these months.

**Table 5**
Differences in mean walleye pollock egg diameter by area within the Gulf of Alaska, April 1982.

| Area | Egg diameter Mean | SE | *N* | SNK grouping |
|---|---|---|---|---|
| Shelikof Strait | 1.397 | 0.003 | 348 | A |
| Semidi Is. to the Shumagin Is. | 1.361 | 0.004 | 348 | B |
| West of the Shumagin Is. | 1.296 | 0.005 | 249 | C |

**Table 6**
Correlation coefficients ($r$) between walleye pollock egg diameter and egg dry weight, and female length, age, body weight, and liver weight.

| | Length | Age | Body weight | Liver weight |
|---|---|---|---|---|
| Egg diameter | 0.210 | 0.245 | 0.080 | 0.171 |
| Egg dry weight | 0.294 | 0.297 | 0.125 | 0.070 |

A significant difference in mean egg diameters was also observed over the course of the spawning season (March–May) in Shelikof Strait (Table 4) in 1981 ($F$ = 23.389, $p<0.0005$), 1982 ($F$ = 16.3387, $0.01<p<0.025$), and 1984 ($F$ = 54.105, $p<0.0005$*). In 1981 and 1984 egg sizes decreased over the course of the spawning season by about 7% per month (Table 4, $0.02<p<0.05$). In 1982, mean egg diameter apparently increased from April to May by 1.4%.

Unpreserved walleye pollock eggs collected from the plankton in the Gulf of Alaska (in April 1987) were larger in diameter ($\bar{x}$ 1.36 mm, range 1.30–1.41) and dry weight ($\bar{x}$ 0.120 mg, range 0.097–0.139) than fresh eggs from Puget Sound (diameter $\bar{x}$ 1.19 mm, 1.03–1.27; dry weight $\bar{x}$ 0.077, 0.052–0.092), which were spawned naturally in laboratory tanks in April 1987. Mean egg diameters from various parts of the spawning range within the Gulf of Alaska were also compared from collections in April 1982 (Table 5). Egg sizes differed among all of the areas examined ($F$ = 18.854, $p<0.0005$). Egg sizes showed a decrease of 7.2% from Shelikof Strait westward to Unimak Pass.

## Relationship between egg size and female characteristics

The mean diameter of hydrated eggs taken from Shelikof Strait females in 1986 was 1.41 mm (range 1.29–1.57). The mean dry weight of these eggs was 0.119 mg (range 0.095–0.148). Variation in egg diameter and egg dry weight among fish was more significant ($p<0.001$) than variation within fish. Correlation coefficients between egg diameter or egg dry weight and female length, age, body weight, and liver weight are presented in Table 6.

The multiple regressions of egg diameter and dry weight against fish length, age, body weight, and liver weight were nonsignificant ($R^2$ = 0.361, $0.10<p<0.25$, and $R^2$ = 0.321, $p>0.25$, respectively). A stepwise regression eliminated all variables as nonsignificant ($p>0.05$). No interactions or nonlinear relationships among variables were found. Fourteen females (29.5–47.0 cm FL) were held in the laboratory to investigate the female length-egg size relationship. As in previous regression analyses, no relationship was seen between female length and egg diameter for these fish (Fig. 2, $r$ = 0.006).

## Spawning characteristics and the relationship of egg size to larval size

The number of egg batches spawned per female in the laboratory in 1987 ranged from 2 to 21 over 3–26 days (Table 7). Excluding the two females which died prematurely, the average number of batches was 14.4 (range 9–21), and the average duration of spawning was 21.4 days (range 18–26). The average interval between batches for all fish was 2.1 days (range 1–5). The relationship between egg diameter and egg dry weight was linear ($p<0.0005$, $R^2$ = 0.630).

*Satterthwaite approximation not used in this test as the criteria were not met. A simple approximation test (Sokal and Rohlf 1981) was used in this case.

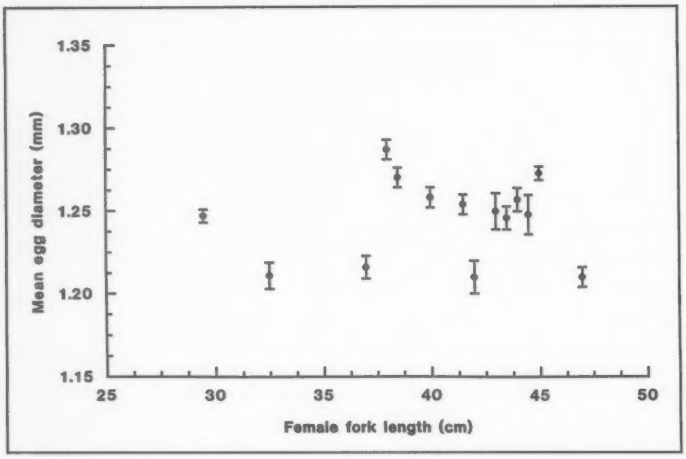


**Figure 2**
Relationship between female fork length and mean egg diameter in walleye pollock. Each dot represents the mean egg diameter from the first batch of eggs spawned from one female in the laboratory. Bars indicate standard error of the mean.

**Table 7**
Frequency and duration of spawning of captive walleye pollock from Puget Sound in 1987.

| Female | Number of batches | Duration of spawning (d) | Interval (d) between batches | | Condition of ovary at death |
|---|---|---|---|---|---|
| | | | Mean | Range | |
| 1 | 9 | 20 | 2.2 | 1–5 | >90% spent* |
| 2 | 2 | 5 | 5.0 | | <10% spent** |
| 3 | 13 | 18 | 1.4 | 1–2 | spent* |
| 4 | 15 | 23 | 1.5 | 1–3 | spent* |
| 5 | 2 | 3 | 3.0 | | <10% spent** |
| 6 | 14 | 20 | 1.4 | 1–2 | spent* |
| 7 | 21 | 26 | 1.2 | 1–2 | spent* |
| Mean | 14.4*** | 21.4*** | 2.1 | | |

*Sacrificed within 1 week of cessation of spawning.
**Died after 2 batches.
***Spent fish only.

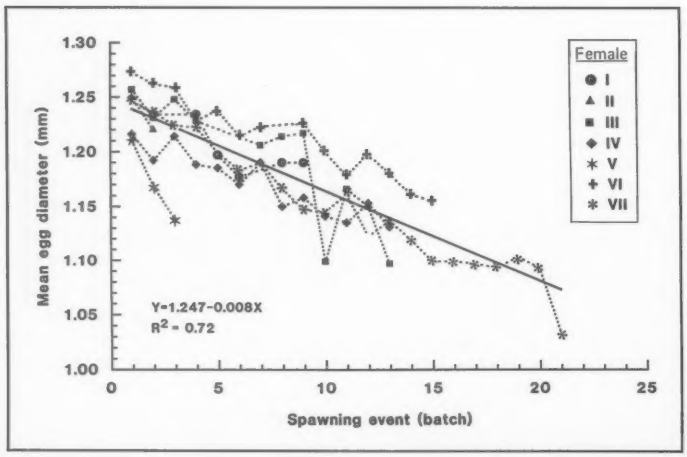


**Figure 3**
Change in mean egg diameter over the batch spawning cycle of female walleye pollock. Solid line indicates fitted regression line. Each symbol represents a separate female held in the laboratory over the spawning cycle.

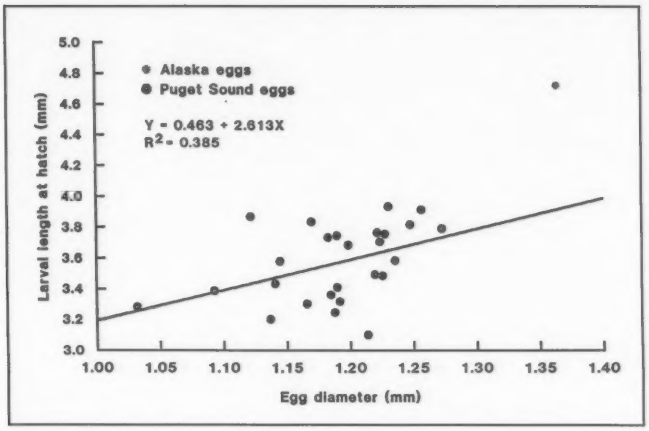


**Figure 4A**
Relationship between mean diameter of a batch of walleye pollock eggs spawned in the laboratory, and the mean standard length of larvae hatched from that batch.

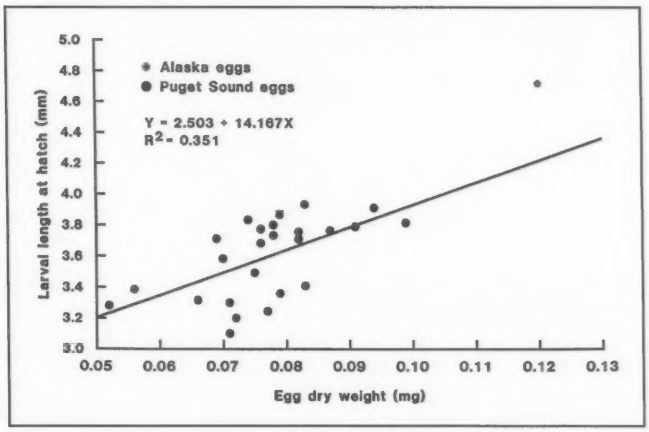


**Figure 4B**
Relationship between mean dry weight of a batch of walleye pollock eggs spawned in the laboratory, and the mean standard length of larvae hatched from that batch.

Mean egg diameter per batch of eggs spawned declined over the spawning cycle of an individual for all females (Fig. 3). The average decline in egg diameter over the batch spawning cycle (for females that completed spawning) was 0.14 mm, or 11.5% of the initial egg diameter.

Thirty-three batches of eggs were incubated and hatched. Larval standard length at hatch was positively correlated with egg diameter (Fig. 4A) and egg dry weight (Fig. 4B). The regressions of larval length at hatch on egg diameter and dry weight were both significant ($0.001<p<0.0025$, $R^2 = 0.385$, and $0.001<p<0.0025$, $R^2 = 0.351$, respectively).

Eighteen batches of larvae were raised to yolk-sac absorption and measured. The relationship between egg size and larval size at yolksac absorption was more variable than at hatch. Both egg diameter and dry weight were significantly correlated with larval length at yolksac absorption ($0.025<p<0.05$ and $0.005<p<0.01$, respectively; Fig. 5A, B).

Egg diameter varied positively with larval dry weight at yolksac absorption (Fig. 6A, $0.0025<p<0.005$, $R^2 = 0.462$), as did egg dry weight and larval dry weight at yolksac absorption (Fig. 6B, $p<0.0005$, $R^2 = 0.852$).

## Discussion

### Characteristics of spawning

The laboratory work from this study supports Sakurai's (1982) evidence that the batch spawning process in walleye pollock (which are partially synchronous spawners; Hinckley 1987) extends over a period of about a month, at least in the laboratory. Sakurai's walleye pollock, however, spawned approximately every 3 days, whereas walleye pollock in this study spawned about every 2 days. This probably reflects the effect of higher water temperatures in this study ($\bar{x}$ 10.1°C, versus 3.5–7.6°C in Sakurai's study). Higher temperatures have been shown to decrease the inter-

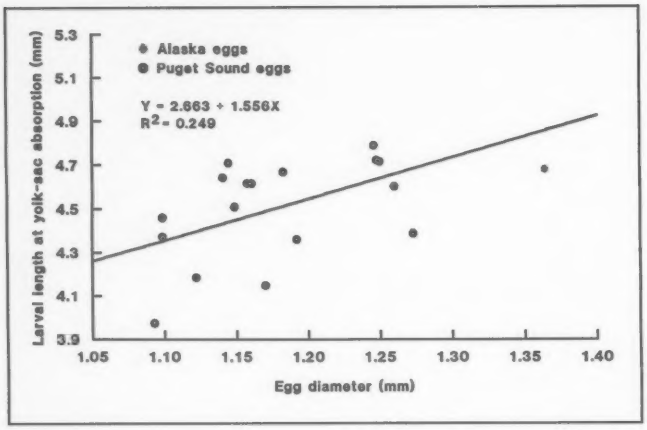


**Figure 5A**
Relationship between mean diameter of a batch of walleye pollock eggs spawned in the laboratory, and the mean standard length of larvae at yolksac absorption.

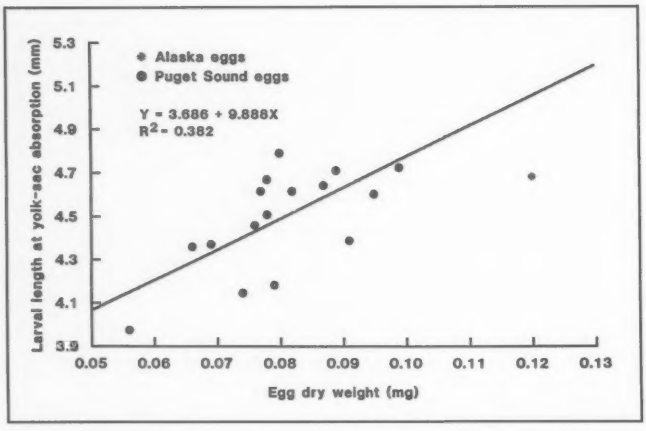


**Figure 5B**
Relationship between mean dry weight of a batch of walleye pollock eggs spawned in the laboratory, and the mean standard length of larvae at yolksac absorption.

val between batches of eggs spawned in Atlantic cod *Gadus morhua* (Kjesbu 1988).

## Egg size variation within and among females

The laboratory studies showed that egg diameter in walleye pollock declined significantly over the spawning period of an individual. This was also shown by Sakurai (1982) for walleye pollock (over a limited portion of the spawning cycle) and for other gadoids by Hislop et al. 1978 and Moksness and Vestergård 1982 (*Melanogrammus aeglefinus*), by Grauman 1965 and Solemdal 1970 (*Gadus morhua*), and Hislop 1975 (*Merlangius merlangus*). The amount of decrease seen in walleye pollock, about 12%, was comparable with that seen in *Gadus morhua* by Kjesbu (1988) (7–15%) and with that in *Merlangius merlangus* by Hislop (1975) (9–14%). This decline may represent an adaptation by the parent stock to conditions faced by the larvae, as discussed later in this section.

Egg size in walleye pollock does not appear to be correlated with female length. The measurement of eggs from the first batch spawned (a method also used by Kjesbu (1988) for *Gadus morhua*) removes variation in egg size caused by the decline in egg size over the course of the spawning cycle, a problem which may have confused the results of other studies of the relationship between egg size and female size. Egg size in walleye pollock did not appear to correlate with female age or condition. Wet weights of body, gonad, and liver are not particularly sensitive indicators of condition in fish, however, and use of these measures may have obscured a correlation between these indices and egg size.

There are many contradictory studies on the egg size-female size relationship. Sakurai (1982, *Theragra chalcogramma*), Marsh (1984, *Etheostoma spectabilis*), Zilstra (1973, *Clupea harengus*), Solemdal (1970, *Gadus morhua*) and Ossthuizen and Daan (1974, *G. morhua*), and others did not find egg size-female size or age

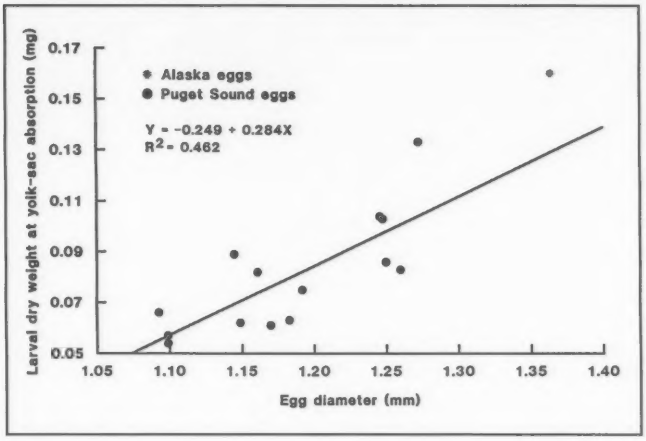


**Figure 6A**
Relationship between mean diameter of a batch of walleye pollock eggs spawned in the laboratory, and the mean dry weight of larvae at yolksac absorption.

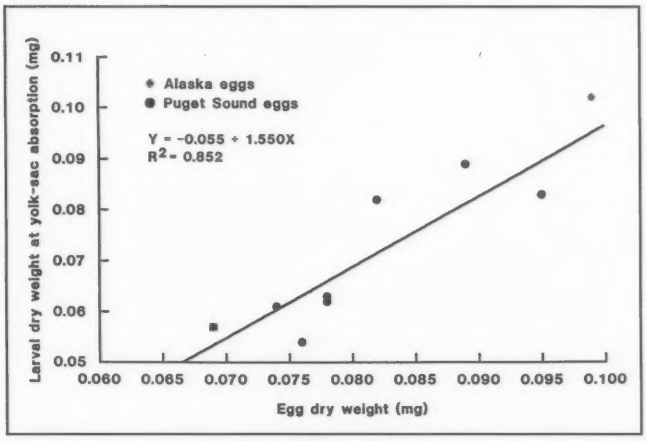


**Figure 6B**
Relationship between mean dry weight of a batch of walleye pollock eggs spawned in the laboratory, and the mean dry weight of larvae at yolksac absorption.

relationships in their studies. On the other hand, there are numerous studies in which egg size-female size relationships have been seen, such as Blaxter and Hempel (1963, *Clupea harengus*), Hislop et al. (1978, *Melanogrammus aeglefinus*), Grauman (1964, *Gadus morhua*), Kjesbu (1988, *G. morhua*), and many on salmonids. Some studies on the same species contradict one another with regards to this relationship. For those species showing a seasonal decline in egg size, an egg size-female size relationship may have been obscured in studies where this was not taken into account.

## Within- and among-population variation in egg size

The population of walleye pollock spawning in Shelikof Strait shows significant seasonal and annual differences in egg size. The seasonal decline in egg size probably covaries with the decline over the spawning cycle. Annual differences in egg size during the peak spawning month (April) in Shelikof Strait appear to be significant. These yearly differences are apparently not attributable to changes in the size or age composition of the spawning stock, as no relationship between these factors and egg size is apparent.

It is possible that differences in the date of peak spawning in different years could change the mean egg size in the first week of April (when eggs measured for this study were collected). There is evidence that the mean date of peak spawning was later in 1986 and 1987 than in some earlier years (Yoklavich and Bailey 1990). The apparent difference in mean April egg size seen in this study could therefore be a reflection of the variability in time between peak spawning and egg collection and the decline in egg size over the spawning season, rather than a true interannual difference.

There appears to be a positive correlation between egg size and latitude in walleye pollock (Table 1). This correlation was also noted by Gorbunova (1954). In this study, this correlation was seen both among widely separated areas such as Puget Sound and the Gulf of Alaska, and within the Gulf of Alaska itself. Latitudinal clines in egg size have been seen by Demir (1963), Chiechomski (1973), and others, and have been discussed by Rass (1941), Marshall (1953), and Thresher (1988). As noted by Thresher, "Latitudinal variation in life histories of marine organisms typically are attributed to selection acting on local populations along a latitudinal environmental gradient..."

Several studies have noted an inverse relationship between egg size and temperature (Southward and Demir 1974, Ware 1977, Marsh 1984, Houghton et al. 1985, Imai and Tanaka 1987). Imai and Tanaka (1987), working with Japanese anchovy *Engraulis japonica*, found yearly changes in egg size which correlated with temperature, and were able, experimentally, to alter egg size during the spawning cycle of anchovy held in the laboratory by changing water temperature. Ware (1977) noted that peak spawning of *Scomber scombrus* occurs later if water temperatures warm more slowly than usual in the spring.

Temperature may be the latitudinal environmental gradient along which selection for egg size acts on local populations. The relationship between latitude and egg size appears to be correlated to temperature in the different spawning regions over the range of walleye pollock (Table 1). In the laboratory experiments on spawning done for this study, ambient water temperature increased over the spawning period, while egg size declined significantly for each female over this period. Mean monthly egg size and mean monthly water temperature at the depth where eggs are spawned (150 m to the bottom) within Shelikof Strait, however, show no apparent inverse correlation. There was also no inverse correlation between mean egg size in April and mean April water temperature at the depth of spawning over the years examined (J.D. Schumacher, Pacific Mar. Environ. Lab., Seattle, WA 98115-0070, unpubl. data). It may be that temperature acts on the parent stock at some earlier date, for example while the stock is migrating to the spawning grounds. Data are insufficient to investigate this question.

## Consequences of egg size variation for larval survival

A correlation between egg size and larval size has also been noted in other species (*Clupea harengus*, Blaxter and Hempel 1963; *Salvelinus alpinus*, Wallace and Aasjord 1984; *Etheostoma spectabile*, Marsh 1986; *Gadus morhua*, Solemdal 1970, Knutsen and Tilseth 1985). Only a few studies have reported no correlation (Zonova 1973, Reagan and Conley 1977, Lagomarsino et al. 1988).

Egg size has been correlated with other larval factors. Growth rate, for example, has been seen to increase with increased egg size (Blaxter and Hempel 1963, Bagenal 1969, Wallace and Aasjord 1984, Moodie et al. 1989). This may be related to increased feeding success due to larger mouth sizes or increased search area (from increased reactive distance or swimming speed). Mouth size has been positively correlated with egg size (Blaxter and Hempel 1963, Shirota 1970, Knutsen and Tilseth 1985). Larvae with larger mouths are able to take larger or more varied sizes of prey items. Length of time from hatch to starvation (due to increased endogenous yolk reserves; Blaxter and Hempel 1963, Bagenal 1969, Theilacker 1981, Marsh 1986, Wallace and Aasjord 1984), and survival (Blaxter and Hempel 1963, Bagenal 1969, Pitman 1979, Small 1979, Moodie et al. 1989) have also been positively correlated with egg size. If larval survival is affected by larval size at hatch (Miller et al. 1988) and other factors, then variation in egg size in walleye pollock may cause differences in larval mortality rates.

It has been proposed that changes in egg size may be an adaptation to the timing of the production cycle, to ensure that larvae are produced that are able to take advantage of the available food supply (Cushing 1967; Hempel and Blaxter 1967; Bagenal 1971; Jones and Hall 1974; Ware 1975, 1977). The reproduction of zooplankton (such as copepods, e.g., *Pseudocalanus* and *Oithona* spp., whose naupliar stages constitute the most common food of first-feeding walleye pollock larvae in the Bering Sea and the Gulf of Alaska; Clarke 1978, 1984; Nishiyama and Hirano 1983; Kendall et al. 1987) is temperature and food related (Checkley 1980a, b; Durbin et al. 1983; Runge 1985; Corkett and McLaren 1978; Landry 1976). This implies that temperature would provide information on the timing of zooplankton reproduction, and therefore on the size of the available larval food supply (Ware 1977). Information on the changes in species and size composition of larval food sources in the western Gulf of Alaska is not presently available. The observed trends in egg size would be explained in terms of larval food supplies if the abundance of prey items increased and the size of food particles decreased and became more uniform as the season progressed.

The observed trends in egg size may also be a result of an adaptation to relieve predation pressure on eggs and larvae. Seasonal changes in egg size could result in changes in the predator-prey size ratio for eggs and larvae, affecting predation rates (Bailey and Houde 1989). This may not be important if egg predators are mainly planktivorous fishes. With zooplankton pred-

ators, however, small changes (10–20%) in egg diameter may affect their ability to handle or consume eggs. Also, if the abundance of egg predators increases, or they co-occur more frequently with eggs, then smaller but more numerous eggs (assuming a tradeoff between egg size and fecundity; Svardson 1949, Bagenal 1978) may be an adaptation to offset higher rates of predation later in the season.

Miller et al. (1988) have shown that predation rates are negatively correlated with larval size, possibly due to differences in predator mouth size, encounter rates of larvae and their predators, or the ability of larvae to escape predators. Trends in egg size and the resulting differences in larval size at hatch may, therefore, also be an adaptation to relieve predation on larvae, if the size, species composition, and co-occurrence of predators and larvae changes seasonally.

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# Estimating Relative Survival Rate for Two Groups of Larval Fishes from Field Data: Do Older Larvae Survive Better Than Young?

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**Abstract.**—Determining absolute survival rates for larval fishes is extremely difficult. However, many ecological questions concern relative survival of two groups. For example, we might ask: (1) Do older larvae have higher survival than younger larvae? and (2) Do faster growers have higher survival than slower growers? We present a simple model and several estimation schemes for the ratio of survival rates based on monitoring relative abundance of the two groups over time. When the logarithm of the ratio of abundances is regressed on time, the resulting estimate of slope is an estimate of the difference in instantaneous mortality rates. An estimate of the ratio of survival rates is obtained by exponentiating the slope. The model is shown to be a logistic model and can be fitted by maximum likelihood methods.

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Determining absolute survival rates for larval fishes is extremely difficult, even when cohorts can be accurately identified by means of daily growth rings in the otoliths. For example, survival between times 1 and 2 might be estimated by catch/tow at time 2 ÷ catch/tow at time 1. Due to random sampling error alone, this estimate may be nonsensical (>1), and the chances of obtaining nonsensical estimates increases with increasing patchiness in the distribution of larvae over space.

In some cases, it may not be necessary to estimate absolute survival rates. Estimates of relative survival rate may be sufficient and easier to obtain. Many ecological questions concern the relative survival rates of two or more groups. For example, at a given point in time, the older larvae present should be larger than the younger larvae and, hence, may have a higher survival rate (Peterson and Wroblewski 1984, McGurk 1986). On the other hand, it has been suggested that larvae born later (i.e., younger larvae) may have a higher survival than larvae born earlier (Victor 1983, Methot 1983, Crecco and Savoy 1985, Rice et al. 1987). Also, it has been suggested that faster-growing larvae survive better than slower-growing ones (Rosenberg and Haugen 1982).

In this paper, we consider how relative survival rates can be estimated for two groups occurring at the same time and place from field data consisting of the composition of the catch at two or more times. The intuitive basis for the method is this: Changes in the relative abundance of two groups over time reflect differences in mortality rates (assuming no emigration or immigration occurs). The methods we present allow for catchability to differ for the two groups and to vary over time. However, the relative catchability (ratio of the catchability coefficients) of the groups cannot change over the time period considered. Thus, if factors such as wind, currents, boat speed, or net clogging vary among sampling periods, then the same proportional change in the catchability coefficient must occur for both groups. This is less restrictive than assuming constant catchability over time (as when estimating absolute survival rate by the decline in catch-per-unit-sampling-effort over time).

## Development of the model

Suppose that at time $t$, a sample of larvae is obtained and that examination of the otoliths reveals that all larvae are of the same (approximate)

age. It is also determined that larvae can be classified as either fast or slow growing on the basis of the widths of the growth increments. Thus, we can determine the proportion of the larvae that are fast growing. If we sample the same population at time $t+1$, we can again separate the larvae into fast- and slow-growing groups on the basis of the width of the otolith at time $t$ (not at time $t+1$).

Alternatively, suppose that a sample of larvae at time $t$ has two cohorts, where a cohort is defined to be all larvae hatching in a given week. We can follow the relative abundance of the two cohorts in the catch over time by taking repeated samples from the population.

We will let the subscripts $E$ and $L$ refer to the two cohorts (e.g., $E$ for early- and $L$ for late-spawned). Let the number of larvae in the population's two cohorts at time $t$ be $N_{Et}$ and $N_{Lt}$. Suppose that the size of each cohort declines exponentially over time such that, for the $i$th cohort ($i \in \{E,L\}$),

$$N_{it} = N_{i0} \exp(-Z_i t)$$

where $Z_i$ is the instantaneous mortality rate (time$^{-1}$) and $N_{i0}$ is the initial abundance of the $i$th group. Also suppose that the expected catch of animals from group $i$ at time $t$ ($C_{it}$), for a standard unit of effort, is proportional to the abundance, i.e.,

$$C_{it} = q_{it} N_{it}$$

where $q_{it}$ is the time- and group-specific catchability coefficient. Then the ratio of expected catches, $R_t$, is

$$R_t = \frac{C_{Lt}}{C_{Et}} = \frac{q_{Lt} N_{L0} \exp(-Z_L t)}{q_{Et} N_{E0} \exp(-Z_E t)}. \quad (1)$$

We assume that the ratio of the catchability coefficients ($q_{Lt}/q_{Et}$) is constant over the course of the study. Since the ratio of initial abundances ($N_{L0}/N_{E0}$) is also a constant, equation (1) can be rewritten

$$R_t = q \frac{\exp(-Z_L t)}{\exp(-Z_E t)} = q \exp\{(Z_E - Z_L)t\} \quad (2)$$

where $q$ is a nuisance parameter that subsumes the catchability coefficients and initial abundances. Taking logarithms of (2) results in a linear relationship with respect to time:

$$\log_e(R_t) = \log_e(q) + (Z_E - Z_L)t. \quad (3)$$

Thus, regressing the logarithm of the observed ratio of abundances ($\hat{R}_t$) against time results in a linear relationship with slope equal to an estimate of the difference in the instantaneous mortality rates. (The proper weighting to use in a weighted regression is discussed below.) Note that it is sometimes necessary to add a small constant to the numerator and denominator to avoid dividing by 0 or taking the logarithm of 0.

Exponentiating the slope estimated by (3) provides an estimate of the ratio of the finite survival rates:

$$\widehat{S_L/S_E} = e^{slope}$$

where $S_L = e^{-Z_L}$; $S_E = e^{-Z_E}$.

By the Taylor's series (delta) method, the asymptotic variance of the estimated survival ratio can be approximated by (Seber 1982):

$$V(\widehat{S_L/S_E}) = e^{(2\ slope)}\ \mathrm{V(slope)}.$$

## Diagnostics

Under the assumptions given above (constant ratio of catchabilities over time and constant difference in instantaneous mortality rates), a plot of the logarithm of the ratio of catches versus time would be expected to be linear (assuming the sample sizes are reasonably large). A departure from linearity suggests violation of one or both of the assumptions. This provides a diagnostic procedure to check on the assumptions. If catchabilities vary in a nonsystematic fashion, the fit of the regressions would be low and would not be influenced by increasing sample size.

## Two-sample estimator

A special case is when only two samples have been obtained. Then, exponentiating the slope of the line described by equation (3) reduces to the change-in-ratio estimator of relative survival described by Paulik and Robson (1969). Thus,

$$\left(\widehat{\frac{S_L}{S_E}}\right) = \frac{\hat{R}_2}{\hat{R}_1} = \frac{\hat{C}_{L2}\,\hat{C}_{E1}}{\hat{C}_{L1}\,\hat{C}_{E2}} \quad (4)$$

where the $\widehat{\ }$ symbol indicates estimated quantities. If the proportion of early spawners in samples 1 and 2 are denoted by $P_1$ and $P_2$, respectively, then an estimate of the variance can be found by the Taylor's series method to be (Seber 1982, p. 382)

$$V(\widehat{S_L/S_E}) = [P_1(1-P_2)]^{-4} \{(1-P_2)^2 P_2^2 V(P_1) + (1-P_1)^2 P_1^2 V(P_2)\}.$$

Here, $V(P_1)$ and $V(P_2)$ are the variances of the proportions, found by the usual formula for variance of a binomial, i.e.,

$$V(P_i) = \frac{P_i(1-P_i)}{N_i}$$

where $N_i$ is the number of larvae in sample $i$, and $i$ can take on the values of 1 and 2.

## Weighted regression

Equation (3) can be seen to be a logistic model by noting that $\log_e(R_t)$ is the logistic transformation. That is, letting $P_t$ be the proportion in the sample at time $t$ which belongs to group "$L$" (i.e., $\frac{C_L}{C_L+C_E}$), the logit transformation of the proportion is

$$\text{logit}(P_t) = \log_e\left(\frac{P_t}{1-P_t}\right) = \log_e(R_t).$$

This allows us to refer to known results for logistic models to determine the optimum weighting scheme.

Not all observations on catch composition are of equal value in estimating the relative survival rate. This is because the variance of the ratio of catches for any particular sampling date will be a function of the sample size and the proportions in the population. One method for specifying weights to be used in the regression, which explicitly accounts for this, is:

$$\text{weight}_t = \hat{C}_{Et}^{-1} + \hat{C}_{Lt}^{-1}.$$

When these weights are used in the regression, the resulting estimates are known as minimum logit chi-square estimates. Once the logistic regression model has been fitted, new weights can be computed using the predicted catch composition, rather than the observed composition. The regression can then be recomputed, the weights updated, and the regression recomputed. until adequate convergence is achieved. This procedure results in maximum likelihood estimates (McCullagh and Nelder 1983). Most standard statistical packages will perform logistic regression so that the user need not specify explicitly the iterative weighting scheme.

The above weighting scheme is appropriate when larvae are sampled randomly, i.e., each larva is sampled independently of all other larvae. This situation is approximated when the expected catch per tow is small ($\leq 1$) and tows are random over space. When the expected catches are large, the sampling procedure results in cluster samples. Consequently, the theoretical binomial variance is too small. However, the binomial variance becomes increasingly small as the sample size increases and as the proportions approach the extremes (0 or 1), and this is what would be expected for cluster sampling. Thus, weights computed from the binomial variance should be reasonably appropriate.

## Estimation when there are many small samples

It sometimes occurs that catch rates are extremely low and many small samples are obtained. For example, sampling may be conducted daily with low intensity. In this case, the logistic regression procedure will not work well due to the occurrence of many zero catches. Estimation under the logistic model can still be accomplished by constructing the likelihood function and solving directly for the difference in mortality rates that maximizes the likelihood function.

The probability that an individual, randomly selected from the catch at time $t$, is from group $E$ (early-spawning group) is equal to

$$\begin{aligned} P_t(E) &= \frac{\hat{C}_{Et}}{\hat{C}_{Et}+\hat{C}_{Lt}} \\ &= \frac{q_{Et}\,N_{E0}\,e^{-Z_E t}}{q_{Et}\,N_{E0}\,e^{-Z_E t} + q_{Lt}\,N_{L0}\,e^{-Z_L t}} \\ &= \frac{1}{1 + qe^{\Delta Z t}} \end{aligned} \tag{5}$$

where $q$ is the "apparent" initial ratio of abundances (actual initial ratio of abundances if the ratio of catchability coefficients is equal to 1) and $\Delta Z$ is the difference in instantaneous mortality rates ($Z_E - Z_L$).

The probability that an animal is from group $L$ is the complement of (5):

$$\begin{aligned} P_t(L) &= 1 - \frac{1}{1 + qe^{\Delta Z t}} \\ &= \frac{qe^{\Delta Z t}}{1 + qe^{\Delta Z t}}. \end{aligned}$$

The likelihood function can then be constructed as the product of the probabilities for each animal in each sample:

$$\begin{aligned} \Lambda &= \prod_{i=1}^{n_E} \frac{1}{1 + qe^{\Delta Z t_i}} \prod_{j=1}^{n_L} \frac{qe^{\Delta Z t_j}}{1 + qe^{\Delta Z t_j}} \\ &= \frac{q^{n_L}\, e^{(\Delta Z \sum_{j=1}^{n_L} t_j)}}{\prod_{i=1}^{n_E+n_L} (1 + qe^{\Delta Z t_i})} \end{aligned} \tag{6}$$

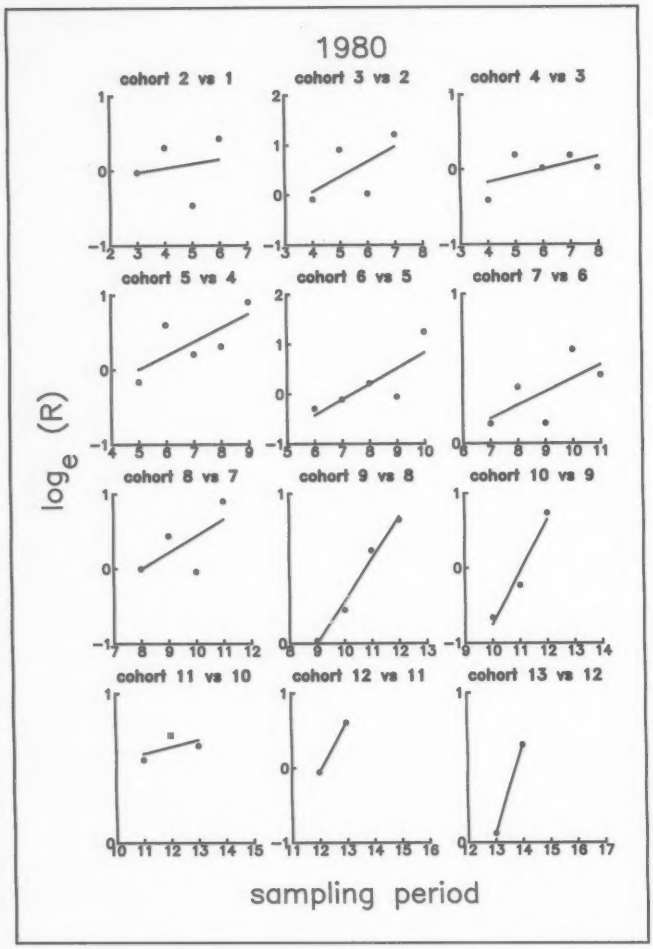


**Figure 1**
Plots of the logarithm of the ratio of abundance (cohort $i+1$ ÷ cohort $i$) versus sampling period (measured as 5-day intervals) in 1980. Slopes of the linear regression lines estimate $Z_E - Z_L$. (Note that the scale of the ordinate varies among plots.) In all 12 comparisons of cohorts, the slope is positive (later cohort has the better survival).

where $n_E$ and $n_L$ are the total number of animals observed in groups $E$ and $L$, respectively, $t_i$ is the time when the $i$th individual from group 1 was caught, and similarly for $t_j$. The major statistical packages have routines for maximizing this function.

### Generalizations

The logistic model is easily extended to enable one to incorporate the effects of covariates. For example, suppose one has information on the time elapsed since the sampling program began ($t$) and also on the number of days ($t^*$) a power plant, which can be an additional source of mortality, has been operating for each of the sampling dates. Then instead of having $t$ as the only explanatory variable, we can have a linear combination of explanatory variables in the exponent

$$\Delta Z t_i + b_1 t_i^*$$

where $b_1$ is the differential mortality rate (per time) of the two groups attributable to power plant operation.

## Example

We consider data on American shad *Alosa sapidissima* in the Connecticut River, Connecticut, USA, kindly supplied by Victor Crecco and Thomas Savoy (Dep. Environ. Prot., Mar. Fish Office, Waterford, CT). A description of the study area and sampling methods, and a careful analysis of the data, are given in Crecco et al. (1983). Our purpose in considering these data is to illustrate the use of our method and to explore the kinds of questions that can be asked by study-

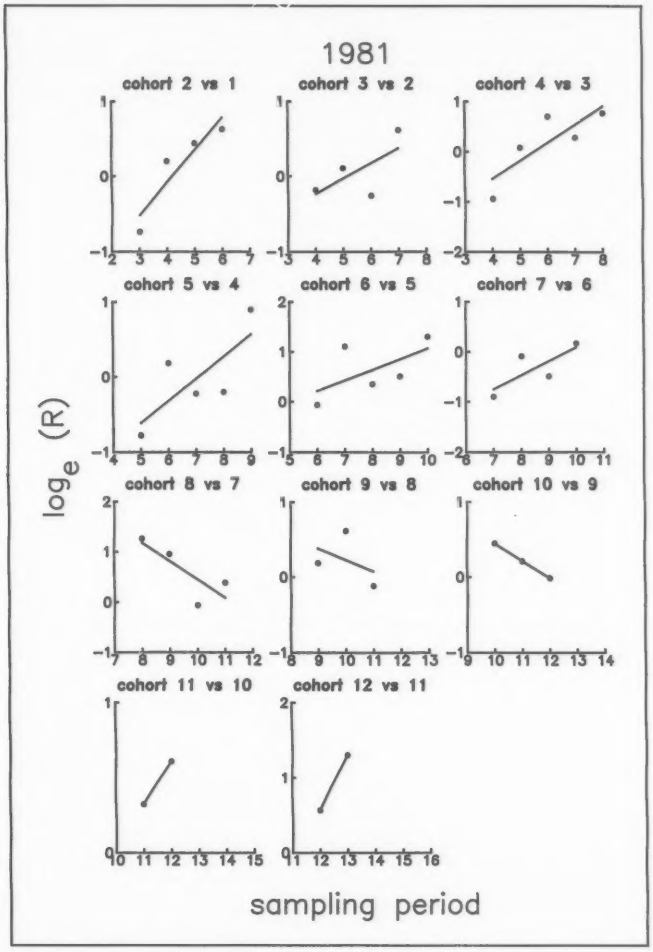


**Figure 2**
Plots of the logarithm of the ratio of abundance (cohort $i+1$ ÷ cohort $i$) versus sampling period (measured as 5-day intervals) in 1981. Slopes of the linear regression lines estimate $Z_E - Z_L$. (Note that the scale of the ordinate varies among plots.) In 8 of the 11 comparisons of cohorts, the slope is positive (later cohort has the better survival).

ing relative survival. For instance, Crecco and Savoy suggest that cohorts spawned later in the season have a higher relative survival based on comparison of larval and juvenile numbers. Our method provides a tool with which we can test this hypothesis for the larval stage while overcoming problems which may be associated with sampling variability or limited sample sizes.

Ichthyoplankton were sampled throughout the spring of 1980 and 1981. Approximately 30–40 larvae were aged for each 5-day sampling period. We compared the mortality of cohort $i+1$ with that of cohort $i$ for all possible $i$ where cohort $i$ is defined to be animals born in the $i$th 5-day period of the season. This resulted in 12 comparisons for 1980 and 11 comparisons for 1981 (Figs. 1, 2). Because information on exact sizes of the samples was not available to us, we computed unweighted regressions. This provides unbiased estimates of the regression parameters, but the estimates are not of minimum variance and the standard errors are not accurate (Weisberg 1980).

The coefficients of determination were poor ($r^2$ range 4–98%, mean 55%, for comparisons with three or more observations) suggesting we cannot place much confidence in the magnitude of the estimates of differential mortality ($Z_E - Z_L$). This is undoubtably due to the very small sample sizes. However, it is worth noting that in 12 of the 12 comparisons using the 1980 data, the differential mortality was positive (see Figure 3), i.e., the survival rate of cohort $i+1$ (the later spawned cohort) was higher than the survival rate of cohort $i$ (the earlier spawned cohort). Also, in 8 out of 11 comparisons using the 1981 data, the later-spawned cohort had the higher survival rate. If there were no differences in survival rates of the two cohorts in each

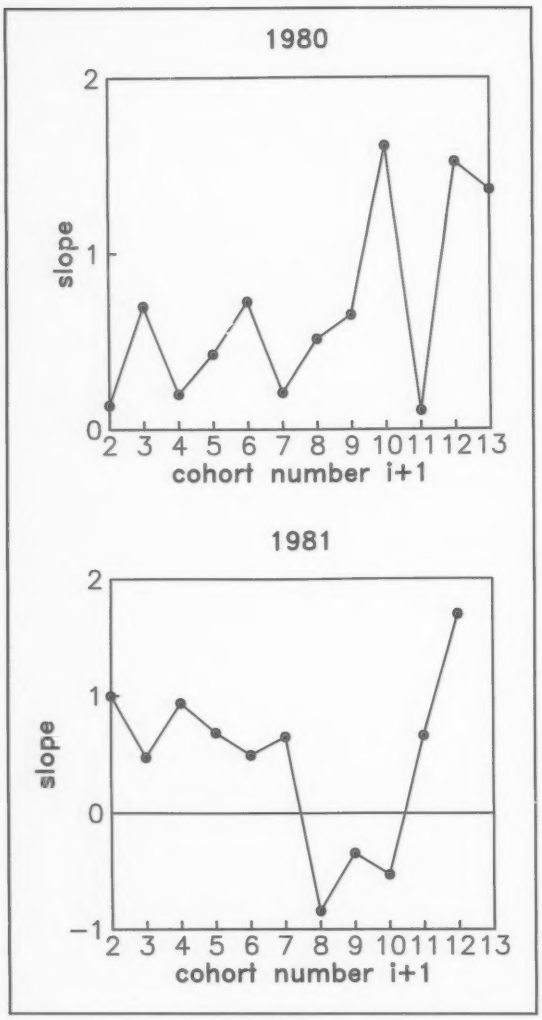


**Figure 3**

Plot of estimated differential mortality (i.e., $Z$ for cohort $i+1$ minus $Z$ for cohort $i$) versus cohort number, $i+1$. Differential mortalities are estimated as the slopes of the regressions in Figure 1 (top) and Figure 2 (bottom). Note that in all but three cases, the later-spawned cohort is estimated to have lower mortality (higher survival) than the earlier-spawned cohort.

pair, then one would expect half the comparisons would have a positive estimate of differential mortality and half would have negative estimates.

## Discussion

We have presented three methods for estimating relative survival rates of larval fishes. The first method is based on a logistic regression model. It provides a graphic way to check the assumptions of constant relative survival and constant ratio of catchabilities. A special case of this method is the two-sample estimator of Paulik and Robson (1969) (our eq. 4). Explicit specification of the likelihood function (eq. 6) is necessary when many small samples are obtained, e.g., from a daily sampling program where the catch per tow is very small.

An intuitive method for estimating relative survival rate would be to estimate the absolute survival rate of each group by the decline in catch-per-unit-effort between two sampling times, and then to take the ratio of the two survival estimates. Thus,

$$\text{alternative estimate of } S_L/S_E = \frac{\frac{\hat{C}_{L2}}{\hat{C}_{L1}}}{\frac{\hat{C}_{E2}}{\hat{C}_{E1}}} = \frac{\hat{C}_{E1}\,\hat{C}_{L2}}{\hat{C}_{E2}\,\hat{C}_{L1}}. \quad (7)$$

The assumption necessary for the estimation of each survival rate is that the catchability has not changed over time. If one were to obtain an estimate of survival that is unfeasible (>1.0) one would be tempted to discard the data without computing relative survival. However, the expression to the extreme right in (7) is exactly equivalent to the two-sample estimator in (4). Thus, one can validly estimate relative survival rates even when estimates of absolute survival are obtained which are nonsensical. This is because the relative survival estimators do not require the catchabilities to remain constant over time, only the relative catchabilities.

On the basis of existing information, it is not possible to state quantitatively in what proportion of fish populations or in which situations late-spawning larvae will survive better than early-spawning larvae. In our example, sample sizes were quite small (~30–40 age determinations per 5-day sampling period) so that estimates of relative survival rate were imprecise. It is interesting to note, however, that in 12 of 12 comparisons in the 1980 data and in 8 of 11 comparisons in the 1981 data the later-spawned cohort (week $i+1$) had a higher survival rate than the earlier-spawned larvae (cohort from week $i$) (Fig. 3). However, our results indicate that late-hatching (smaller) larvae survive a given calendar period better than early-hatching (larger) larvae which is opposite to the general findings that larval fish mortality rates decrease with increasing size and/or age (Peterson and Wroblewski 1984, McGurk 1986). This suggests that whatever the cause of mortality (e.g., predation, transport), the vulnerability of larval shad in the Connecticut River to this factor increases with age and/or size during the period studied.

Our method was developed for the situation in which cohorts can be sampled simultaneously. Thus, if in a particular week gear efficiency was better than normal, any changes in catchabilities would tend to affect both cohorts so that the ratio of catchabilities might stay relatively constant. It may be tempting to use our method to compare cohorts over the same part of the ontogeny (i.e., cohorts of the same age occurring at different times of the season). However, in this situation there is no reason to believe that variations in catchability over time of the first cohort will be tracked by variations in catchability of the later cohort. Hence, there is no advantage in using our method over traditional methods of estimating absolute survival based on declines in catch-per-unit-effort.

Finally, we note that methods for estimating relative survival have wide applicability beyond the study of larval fishes. A classical problem is Lee's phenomenon in which back-calculated sizes at the first annulus do not agree with the observed sizes of the young fish. Jones (1958) proposed as explanation that faster-growing fish may have a different mortality rate than slower growers. This can be studied by observing the proportion at each age that have a small back-calculated size at the first annulus. Hoenig and Lawing (1983) describe how the logistic model might explain the occurrence of progressively skewed sex ratios with age. Differential survival has been studied by a variety of mark-recapture methods in the context of fitness and natural selection (see Manly 1985) and as a means of estimating impacts of power plants (see Burnham et al. 1987). Another application is to the evaluation of stocking success as related to genetic strain of fish or hatchery treatment. That is, the ratio of abundances of two strains can be monitored over time to study whether one strain survives better than the other.

## Acknowledgments

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# Horizontal and Vertical Movements of Yellowfin and Bigeye Tuna Associated with Fish Aggregating Devices*

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**Abstract.**—The horizontal and vertical movements of yellowfin tuna *Thunnus albacares* and bigeye tuna *T. obesus* captured near fish-aggregating devices (FADs) were determined using pressure-sensitive ultrasonic transmitters. The movements of these FAD-associated fish were compared with the tracks of yellowfin tuna not associated with FADs. Tracks from 11 yellowfin and 4 bigeye tuna were obtained; these included 23 complete 24-hour periods of observation. Whether associated with FADs or a 40-fathom (75-m) reef dropoff, most yellowfin and bigeye tunas exhibited similar diurnal patterns. The fish tended to remain tightly associated with FADs or the reef dropoff during the day, move away at night, and return the next morning. The maximum range of these nighttime excursions averaged approximately 5 nmi. These tunas apparently treated the FADs as outliers of the coastal topography. This may not be the same behavior that results in the association of these species with drifting objects such as logs. Tuna can learn FAD positions and navigate precisely between FADs that are at least 10 nmi apart. When not associated with FADs or the 40-fathom dropoff, yellowfin tuna oriented to the bottom of the mixed layer (50–90 m) in daytime, whereas the bigeye occupied depths between 190 and 250 m. The daytime distribution of bigeye tuna seemed to be influenced by the depth of the 15°C isotherm. Both species swam closer to the surface at night. Swimming strategies possibly associated with energy and thermoconservation were observed.

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Tropical and subtropical pelagic fishes aggregate around natural, drifting debris such as logs and mats of algae. Man-made, anchored floating objects, known as fish aggregating devices (FADs), have also proven effective in attracting and holding commercially important pelagic species (Shomura and Matsumoto 1982, Matsumoto et al. 1981, Brock 1985). Species commonly found around FADs in Hawaii are yellowfin tuna *Thunnus albacares*, bigeye tuna *T. obesus*, skipjack tuna *Katsuwonus pelamis*, dolphin or mahimahi *Coryphaena hippurus*, and wahoo or ono *Acanthocybium solandri*. The first commercial FADs were deployed in the calm waters of the Philippines in the early 1970s to attract yellowfin tuna (Kihara 1981), and in 1977 experimental FADs designed for use in high-energy, deep-water environments were anchored around the Hawaiian islands (Matsumoto et al. 1981). Due to the success of these bouys in aggregating fish, FADs have come to play an important role in the commercial, subsistence, and recreational fisheries of all the tropical and sub-tropical oceans of the world.

Despite the widespread use of FADs, left unanswered are important questions concerning their range of influence, optimal placement, and impact on surrounding fish populations. The behavioral patterns that result in fish being associated with floating objects of any type are poorly understood and not widely agreed upon (Gooding and Magnuson 1967, Hunter and Mitchell 1967, Fedoryako 1982). However, the underlying mechanisms of aggregation have generally been assumed to be the same for both free-floating phenomena such as logs, and anchored man-made objects such as FADs (Shomura and Matsumoto 1982). To better understand the behavior of tunas associated with FADs, the movements of yellowfin and bigeye tuna caught within 500 m of these devices were tracked using pressure-sensitive ultrasonic transmitters. The movements of these fish were compared with those of tunas that were not associated with FADs, but with the reef perimeter surrounding the islands. In Hawaii and elsewhere in the Pacific, yellowfin tuna can be found in the vicinity of the 40-fathom (75-m) isobath where the island topography abruptly descends into very deep water. In fact, the dropoff of the outer reef edge is often so steep that

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the horizontal distance between the 40-fathom and 100-fathom (187-m) isobaths is measured in tens of meters. To observe the behavior of non FAD-associated tuna, three yellowfin tuna were tracked that were caught on or near the 40-fathom isobath around Oahu, Hawaii.

The influence of FADs on the vertical movements of these species was investigated by comparing the depth distributions of the two species in on-FAD (within 500 m of a FAD) and off-FAD (beyond 500 m of a FAD) situations. The depth distributions were analyzed with respect to ambient ocean temperatures, as measured by expendable bathythermographs.

## Methods

The horizontal and vertical movements of individual fish were monitored by pressure-sensitive, 50 KHz ultrasonic transmitters (Vemco, Halifax, Nova Scotia, Canada). Fish caught on the tracking vessel by trolling and pole-and-line techniques were fitted with transmitters by passing two nylon "tie-wraps" through the dorsal pterygiophores and trunk musculature adjacent to the second dorsal fin (Fig. 1). The fish were out of the water for approximately 1 minute during this procedure. The fish were then released and followed using a directional hydrophone mounted on the tracking boat. Whenever possible, a distance of approximately 200 m was maintained between the fish and the boat. Geographic position was determined every 15 minutes by a combination of Loran-C, radar, bathymetric, and visual fixes. These techniques evolved from pioneering work in tuna tracking by Yuen (1970), Laurs et al. (1977), Carey and Olson (1982), and Carey (1983). A summary of previous ultrasonic tracks of tuna has been compiled by Hunter et al. (1986). A detailed account of the methods used in the current study has been published previously (Holland et al. 1985, Bayliff and Holland 1986).

The transmitters were equipped with pressure sensors, which modulated the rate of pulse transmission in response to changes in water pressure (depth). Thus, vertical movements of the fish were determined by measuring the time between signal pulses. These pulses were recorded on audiocassettes for analysis ashore. Expendable bathythermographs deployed approximately every 3 hours provided ocean temperature profiles, which were superimposed on the vertical movement plots. Pooled time-at-depth and time-at-temperature histograms were constructed from all tracks combined, using 10-m and 1°C bins averaged every 10 minutes. The data were analyzed for daytime and nighttime depth distributions. Differences in the temperature and depth distributions for day-versus-night and on-FAD versus off-FAD were analysed by factorial analysis of variance (SAS General Linear Models Procedure, SAS 1985). Portions of tracks occurring on-FAD or near the reef dropoff were not included in these calculations. Thus, the depth histograms and overall averages are compiled from movements that were not constrained by bottom topography or influenced by the presence of floating objects.

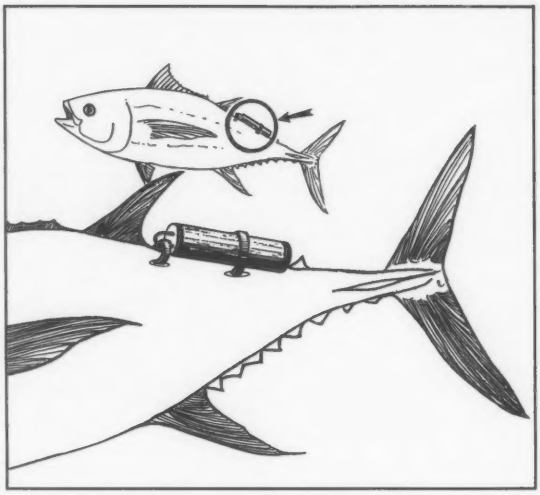

**Figure 1**
Transmitters were attached to yellowfin and bigeye tuna with two nylon straps inserted through the dorsal musculature and pterygiophores associated with the second dorsal fin (from Holland et al. 1985).

The tracking techniques used in this study are not capable of detecting small-scale changes in the horizontal swimming direction of the fish. Consequently, sustained swimming speeds have been calculated only from sections of tracks in which fish demonstrated prolonged straight-line movements. Swimming speeds were calculated as distance traveled per unit time and in terms of body lengths (fork length, FL) per second. Swimming speeds were calculated for each complete hour of "staight" running; these hourly rates were averaged to yield a sustained swimming speed for the relevant section of each track. Vertical movements were not included in these calculations.

Daytime and nighttime time-at-temperature histograms were generated for both yellowfin and bigeye tuna. Because of differences in absolute ocean-surface temperatures between different tracks, and because of

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previous indications that ocean thermoclines may be important orientation cues for tuna (Carey and Olson 1982), the time-at-temperature data were analyzed relative to the surface mixed layer. Thus, the mixed layer is referred to as ML, and the progressively colder 1°C isotherms as ML-1, ML-2, and so on.

## Results

The results reported here are from tracks of 11 yellowfin and 4 bigeye tuna. Duration of tracks from release to track termination ranged from 5 hours to 6 days, with an average duration of 31.6 hours. Overall, these tracks encompass 23 complete 24 hour periods of observation. All 4 bigeye and 8 of the 11 yellowfin tuna were caught within 500 m of FADs. The remaining three yellowfin tuna tracks were from fish caught on or near the 40-fathom contour around the island of Oahu.

### Horizontal movements

For yellowfin tuna, a clear pattern of horizontal movement was apparent. That is, during daylight the fish usually moved within a home range, staying in proximity to certain well-defined physical features, such as FADs or the outer reef dropoff. Eight of the 11 yellowfin tuna and 2 of the bigeye tuna showed aspects of this behavior, and this pattern was exhibited by both the FAD-associated and coastline-associated fish. Most of these fish made diurnal movements away from these daytime haunts, with the initial change in location often occurring around sunset.

**FAD-associated yellowfin tuna** These tuna spent daylight hours very close to the FADs, and then left those locations sometime between late afternoon and early nighttime to embark on extensive nighttime excursions, returning to the same or another FAD the following day. Five of the eight FAD-associated yellowfin tuna displayed aspects of this diurnal on-FAD and off-FAD behavior. A sixth FAD-associated fish showed signs of displaying this behavior, but was lost before this could be confirmed. The following is a brief synopsis of their horizontal movements.

Yellowfin tuna YF8404 (51 cm FL) was caught and tagged at V FAD at 0927, and stayed within 100 m of the FAD for 11.3 hours before leaving it a few minutes after sunset (1925, Fig. 2A). The fish then made a nighttime excursion totaling 12 nmi before returning to within 100 m of the FAD by 1312 the next day. During the last few hours of this approach the fish moved very slowly, as if it was drifting in the prevailing current. Once at the FAD, the fish again stayed close to the buoy until departing at sunset on a second

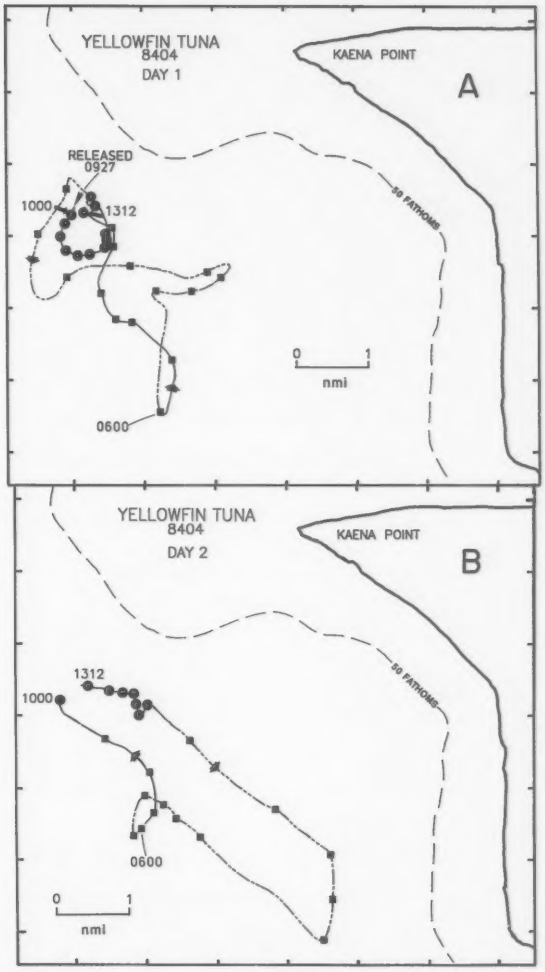


**Figure 2**
(A) 48-hour track of yellowfin tuna YF8404 tagged and released at 0927 at V FAD, Oahu. Circles = hourly marks when fish is on-FAD; squares = hourly marks when fish is off-FAD. In this and subsequent figures, solid line = daytime movements, dashed line = nighttime movements, and marks on figure axes = 1° divisions. On the first day (A) the fish remained very close to the FAD as it moved in a circular path in the current, departed the FAD after nightfall, and returned at 1312 the following day. The second day's behavior (B) was similar, despite a different pattern of movement by the FAD.

nighttime excursion of 11.25 nmi. The maximum distance away from the FAD was 3.0 nmi on the first night and 5.0 nmi on the second. On both excursions, the fish commenced moving back toward the FAD immediately after sunrise (Fig. 2A, B).

Two hours after fish YF8504 (47 cm FL) was tagged and released at S FAD at 0551, it made a 4-hour, 1-nmi excursion away from the buoy before taking up a posi-

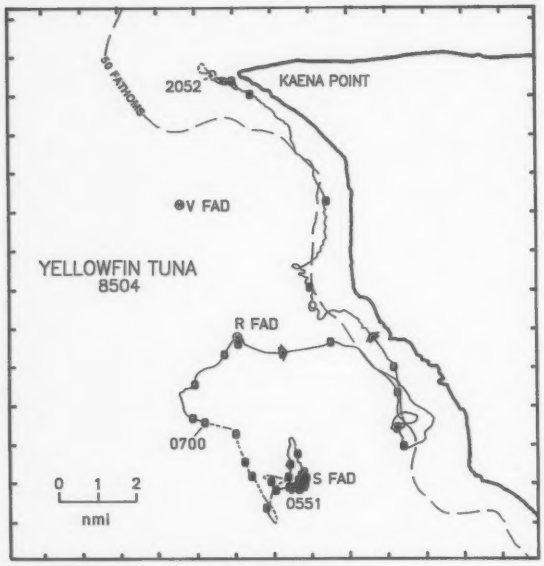


**Figure 3**

Yellowfin tuna YF8504 spent 8 daylight hours on the upcurrent side of S FAD before moving away at night. The next morning it moved to R FAD until disturbed by a school of porpoises, when it immediately took a direct course to the island dropoff, which it patroled for the rest of the day. In this and subsequent figures, squares = hourly position marks.

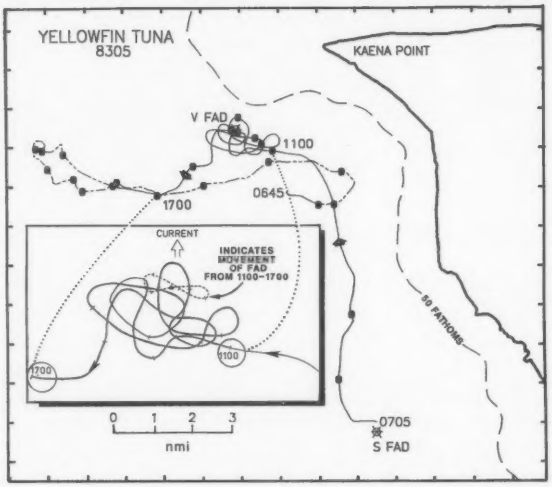


**Figure 4**

Yellowfin tuna YF8305 departed S FAD immediately after release at 0705 and took a direct course to the next nearest FAD, V (R was off station at the time), where it patroled almost exclusively in the upcurrent area (insert) before making an overnight excursion totaling 15 nmi.

tion within 50 m of the FAD for the remaining 8.0 hours of daylight (Fig. 3). During this time the fish was almost exclusively on the upcurrent side of the bouy. At 2345 the fish left the FAD and moved offshore; by sunrise the next day, it was 3.25 nmi from S FAD. The fish then moved 3.0 nmi in a direct course to the nearest adjacent FAD (R) arriving there at 0910. Once there, it stayed extremely close to the FAD and in the company of a school of other yellowfin tuna that could be seen from the surface. At 1020 a group of porpoises arrived and dove through the school of tuna, which appeared to scatter in all directions. The tagged fish dove and swam to the 40-fathom contour of the island, where it stayed for the rest of the day. Contact was lost just after sunset on the second night.

Fish YF8305 (55 cm FL), after being tagged and released at S FAD at 0705, swam for 4.0 hours on a direct course to V FAD, approximately 10 nmi away from the release point (Fig. 4). The fish spent 95% of the next 5.0 hours moving around on the upcurrent side of this FAD. In the late afternoon, the fish departed the FAD and spent most of the night farther offshore, moving in a 15-nmi loop before heading back toward V FAD the following morning. Just after first light, when the fish had returned to within 2 nmi of the FAD and appeared to be headed back even closer, the transmitter was shed.

The tracks of fish YF8406 (62.5 cm FL) and YF8501 (44.0 cm FL) were similar. During the daytime, both fish stayed very close to their respective FADs (for 9 and 12 hours, respectively), and both were lost at sunset in deteriorating sea conditions. Because there was no evidence of transmitter failure, and exhaustive searches at the FAD locations after dark failed to relocate the signal, it is reasonable to assume that both these fish were lost when they made sudden evening departures from the vicinity of their respective FADs.

Fish YF8302 (64 cm FL) was caught and tagged at S FAD, but lost 5.0 hours later. When contact was lost, the fish had departed the release site, but appeared to be curving back toward the bouy.

Fish YF8502 (74.5 cm FL) was similar to other FAD-associated yellowfin tuna in that, for the first 5.0 hours of the track (0600–1100), it stayed in close proximity (within 100 m) to S FAD. However, it then moved steadily away but was lost 12 nmi southwest of the buoy due to equipment failure after 13.5 hours of track and before any possible long-term trend had become apparent.

Fish YF8506 (75.25 cm FL) was caught near S FAD at 0630. Unlike the other FAD-associated yellowfin, it immediately began to move steadily away, maintaining a constant southwest course for the next 17.5 hours, at which time the track was terminated (Fig. 5).

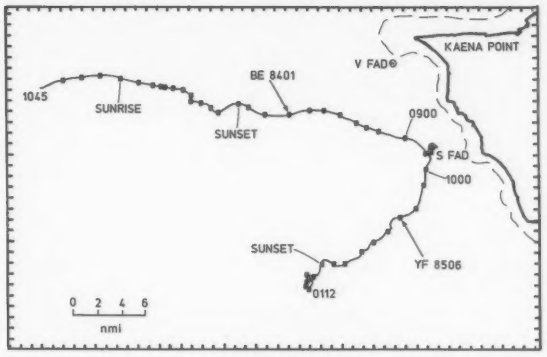


**Figure 5**

Bigeye BE8401 and yellowfin tuna YF8506 both departed S FAD almost immediately upon release and maintained quite straight azimuths at constant speeds. During darkness, both fish slowed down, and YF8506 became more variable in swimming direction.

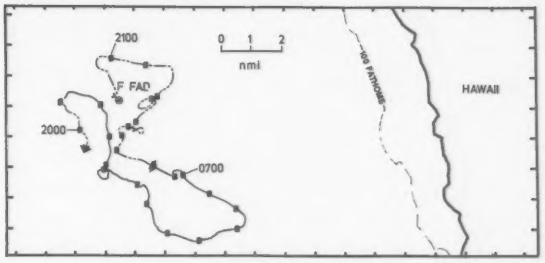


**Figure 6**

Caught and released after sunset at F FAD off the Kona coast of Hawaii, bigeye tuna BE8205 made a 24-nmi overnight loop before returning to the FAD by late afternoon of the following day.

**FAD-associated bigeye tuna** Four tracks were made of bigeye tuna caught near FADs. Of these four, one was lost after a few hours and before any diurnal patterns became apparent, one moved continuously away from the FAD (Fig. 5), and two displayed diurnal on-FAD and off-FAD behavior similar to that exhibited by the yellowfin tuna. The following is a synopsis of these two tracks.

Bigeye tuna BE8205 (74.5 cm FL) was caught and tagged 200 m from F FAD off Kona, Hawaii, about 1 hour after sunset (Fig. 6). Upon release, it proceeded on a 24.0-nmi overnight excursion which took it away from the FAD, before gradually reapproaching the FAD in the afternoon of the next day. The maximum distance it moved away from the FAD was 5.75 nmi. This track was then terminated after 24.0 h.

Fish BE8706 (72.0 cm FL) was caught at first light within 50 m of C FAD located off Kealakekua, Hawaii. The fish remained extremely close to the bouy throughout the day until 1 hour after sunset, when it made a 2-nmi excursion that lasted approximately 3 hours. The fish then returned to the immediate vicinity of the buoy, where it remained for the rest of the night and at least through noon of the following day, when the track was terminated after 30.0 hours.

**Coastline-associated yellowfin tuna** Three tracks were made of yellowfin tuna caught on the reef dropoff on the west coast of Oahu in water between 40 and 50 fathoms (75–95 m) deep. These fish were in the same size range as those caught around the FADs, and tracks spanning 6 days, 36 hours, and 37 hours were obtained, which encompassed a total of six day-night transitions. Two of the three fish displayed offshore excursions every night that they were tracked (a total of five nights). These tracks were as follows.

Fish YF8303 (70.0 cm FL) was caught and tagged at 0855 about 0.75 nmi off the leeward coast of Oahu on the 40-fathom dropoff (Fig. 7A). For the next 7 hours, the fish remained on or near the 40-fathom dropoff, before moving slightly further offshore in the late afternoon. During the subsequent 12 hours of darkness, the fish made a 17-nmi offshore excursion before returning to the 40-fathom contour in the second hour of daylight on the following day. The maximum distance away from the point at which it reencountered the dropoff was approximately 8.25 nmi. The fish remained on the reef slope for the remaining daylight hours until contact was lost at 1130, after 26 hours of tracking.

Forty-eight hours after contact was lost, a hydroacoustic search of the 40-fathom contour reestablished contact with the fish, and the track was resumed at 1426 of the third day (Fig. 7B). The fish spent the remaining daylight hours moving back and forth along the dropoff before moving offshore in late afternoon. The fish spent all night on a 13-nmi excursion before returning to the 40-fathom contour at first light on the next day. The greatest distance from the point of return to the dropoff was approximately 5.25 nmi. The track was suspended at 0730 on the fourth day. The fish was relocated on the 40-fathom isobath on the afternoon of the following (fifth) day at 1642 (Fig. 7C). Again, the fish moved offshore in the late afternoon and spent all night in deeper water on a 7.5 nmi excursion. Maximum distance from the point of return to the dropoff was 3.3 nmi. The time of arrival back at the 40-fathom contour was within 1 minute of the time of arrival on the previous day (Fig. 7B,C). The track was terminated at 0630 on the sixth day because of an impending storm. In summary, this fish was tracked over three day-night-day cycles spanning 6 days and, on each occasion, it made a nighttime off-

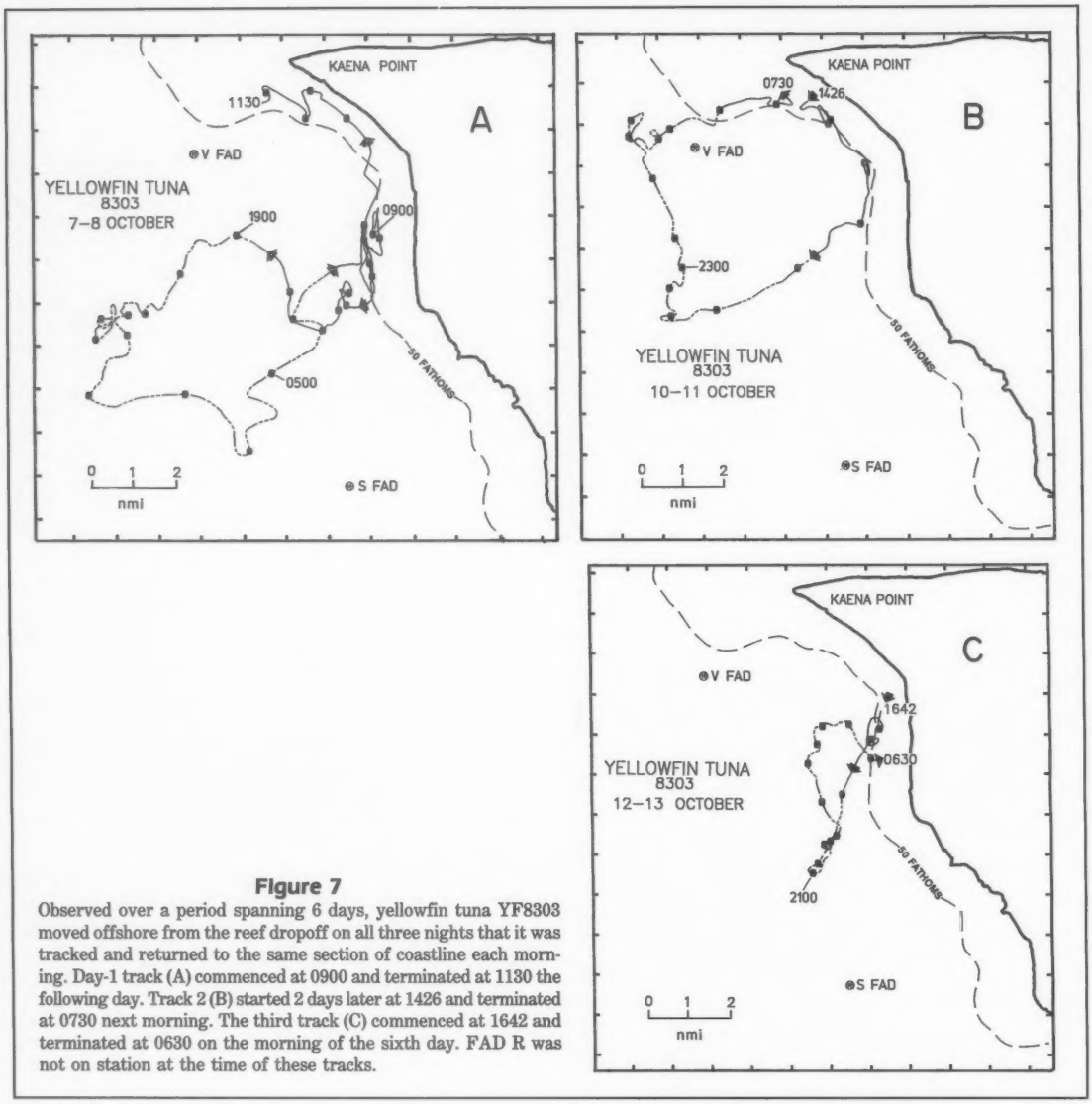


**Figure 7**

Observed over a period spanning 6 days, yellowfin tuna YF8303 moved offshore from the reef dropoff on all three nights that it was tracked and returned to the same section of coastline each morning. Day-1 track (A) commenced at 0900 and terminated at 1130 the following day. Track 2 (B) started 2 days later at 1426 and terminated at 0730 next morning. The third track (C) commenced at 1642 and terminated at 0630 on the morning of the sixth day. FAD R was not on station at the time of these tracks.

shore excursion followed by a return to the 40-fathom contour on the following morning.

Fish YF8503 (47 cm FL) was caught on the 50-fathom contour at 1200 and stayed in this vicinity for 7.0 hours before moving offshore in the late afternoon to make a 24-nmi nighttime excursion (Fig. 8). The next morning, the fish returned to within 0.5 nmi of the section of coastline it had left the previous evening, the maximum distance from the point of return being 9 nmi. The tracking was temporarily suspended at 0930 and resumed at 1150, when the fish was relocated on the 40-fathom contour near Kaena Point. From here the fish embarked on a prolonged and constant run around the point and along the 40–50 fathom contour of the north shore of Oahu. At sunset of the second day, the fish again moved offshore. When contact was lost at 0100, the fish was 7.5 nmi offshore.

Fish YF8405 (57 cm FL) was caught on the 50-fathom contour and patroled this area for about the next 24 hours. This fish did not move offshore at night. Tracking was suspended at 0715 the second day, but resumed at 1715 the same evening when the fish was

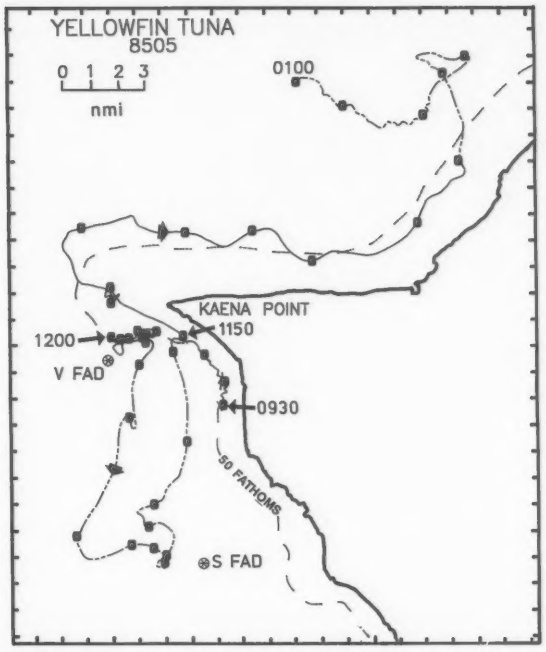


**Figure 8**

Yellowfin tuna YF8503 moved offshore and made a complete loop during the first night. Tracking was suspended between 0930 and 1150 of the second day. During the second day it swam at a constant pace along the reef dropoff bordering the north shore of Oahu before again heading offshore after sunset on the second night. This demonstrates that the diurnal onshore–offshore pattern is not site-specific to the west coast of Oahu. Contact was lost at 0100.

relocated on the 40-fathom contour. At times, the fish moved into water less than 30 m deep, but was lost just after sunset when the transmitter battery failed. However, this fish was caught two weeks later by a fisherman trolling at R FAD, 7 nmi away from the initial release point.

Combining the FAD-associated and coastline-associated fish, 7 of the 11 yellowfin tuna demonstrated diurnal behavioral patterns in which daytime haunts were abandoned at night. These 7 fish were observed to make a total of 11 nighttime departures from daytime locations. Of those 11 nighttime excursions, 7 were demonstrated to be completed loops wherein the fish returned to their original starting points. In addition, two FAD-associated bigeye tuna completed two nighttime-initiated loops. For the yellowfin tuna, the average maximum distance away from the following morning's destination was 5.28 nmi (SD = 1.9, N = 7). When the two documented bigeye tuna loops are included, the average maximum distance is 4.97 nmi (SD = 2.0, N = 9).

**Swimming speeds** Unlike the majority of the fish, one bigeye (BE8401) and one yellowfin tuna (YF8506) almost immediately departed their respective FADs and continued to swim away along straight azimuths for the entire duration of the tracks (Fig. 5). Consequently, large sections of these tracks were included in calculations of sustained swimming speeds. Daytime sustained swimming-speed data are summarized in Table 1.

The greatest distance traveled in 1 hour was exhibited at night by YF8503 which traveled 5.0 nmi. This is equivalent to 2.57 m (4.6 body lengths) per second (Fig. 8). When YF8504 was driven away from R FAD by a porpoise school, it swam the first half-hour towards the 40-fathom contour at a rate of 1.32 m (2.4 body lengths) per second (Fig. 3).

**Table 1**

Daytime sustained swimming speeds of selected yellowfin (YF) and bigeye (BE) tunas.

| Track number | Fork length (cm) | Segment duration (h) | Average hourly speed (±SD) m/s | Average hourly speed (±SD) Body lengths (FL)/s |
|---|---|---|---|---|
| YF8506 | 72.25 | 10.0 | 0.89 ± 0.15 | 1.19 ± 0.20 |
| YF8502 | 74.50 | 7.0 | 0.95 ± 0.10 | 1.28 ± 0.14 |
| YF8503 | 56.00 | 6.0 | 1.80 ± 0.38 | 3.20 ± 0.68 |
| YF8305 | 54.50 | 4.0 | 1.32 ± 0.24 | 2.40 ± 0.40 |
| | | YF Mean = | 1.24 ± 0.41 | 2.01 ± 0.96 |
| BE8401 | 57.00 | 13.0 | 0.79 ± 0.20 | 1.38 ± 0.35 |
| | | Combined mean = | 1.15 ± 0.41 | 1.89 ± 0.88 |

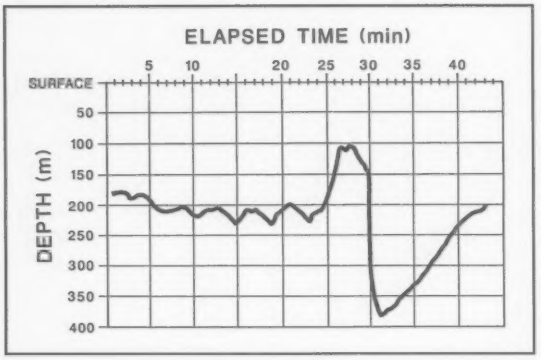


**Figure 9**

Fine-scale behavior of bigeye tuna BE8401 shown by 45-minute segment of vertical movements transcribed from data tape, including a rapid dive of 230 m in 1 minute, a rate equivalent to 6.7 body lengths/second. Ambient temperature at the maximum depth of 380 m was 9°C.

## Vertical movements

The tape recordings of the pulsed signal from the transmitters resulted in detailed, continuous plots of vertical position. Rapid and small-scale changes in depth were discernible (e.g., Fig. 9), as were longer-term diurnal shifts in vertical distribution.

**Day-night depth distributions** In general, yellowfin tuna swam closer to the surface during darkness. For example, a dramatic change in the depth of swimming of fish YF8305 occurred exactly at sunset and lasted until first light the following morning, when it again began to swim deeper (Fig. 10). Combining all the offshore and off-FAD portions of the yellowfin tuna tracks yielded an average daytime depth of 71.3 m (±42.0 SD, $N = 333$), whereas the average nighttime depth was 47.3 m (±33.1 SD, $N = 444$). These daytime and nighttime depth distributions (Fig. 11A, B) are significantly different (ANOVA, $p = 0.0001$). However, this analysis also indicates significant variability among individual tracks.

Bigeye tuna swam at significantly greater daytime depths than the yellowfin tuna, and showed even greater shifts between daytime and nighttime distributions. When off-FAD, the predominant bigeye tuna daytime distribution was between 220 and 240 m, whereas the predominant nighttime depth was between 70 and 90 m (Fig. 12A, B).

**On-FAD versus Off-FAD depth distributions** Swimming depths of five yellowfin and one bigeye tuna that were on- and off-FAD during daytime hours support the proposition that FADs tend to bring the fish closer to the surface than they would normally be in other offshore parts of the ocean. These tracks were analyzed to determine if significant changes in depth distribution occurred when the fish were aggregated around the FADs, independant of diurnal influences. When on-FAD, three of the yellowfin tuna were closer to the surface than when off-FAD, one showed no change in depth, and one was deeper. Pooling these data for this subset of yellowfin tuna gave a mean on-FAD depth of 59.3 m (±30.7 SD, $N = 225$), which is significantly different from the mean off-FAD depth of 85.2 m (±52.0 SD, $N = 239$).

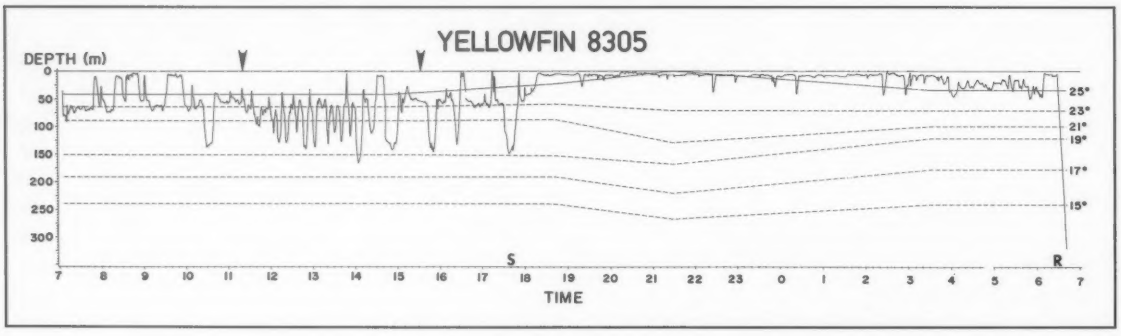


**Figure 10**

Plot (24-hour) of vertical movements of yellowfin tuna YF8305. In this and subsequent figures, S = sunset, R = sunrise. Arrows denote the beginning and end of time spent at V FAD. Before and after this period, the fish exhibited the "traveling" behavior of making abrupt shifts between the surface and the top layers of the thermocline. Once at the FAD, the vertical behavior became predominantly sinusoidal. All dives made both on- and off-FAD had a consistent floor around 20°C between 140 and 150 m. The rapidly descending trace at end of plot denotes the tag being shed from the fish.

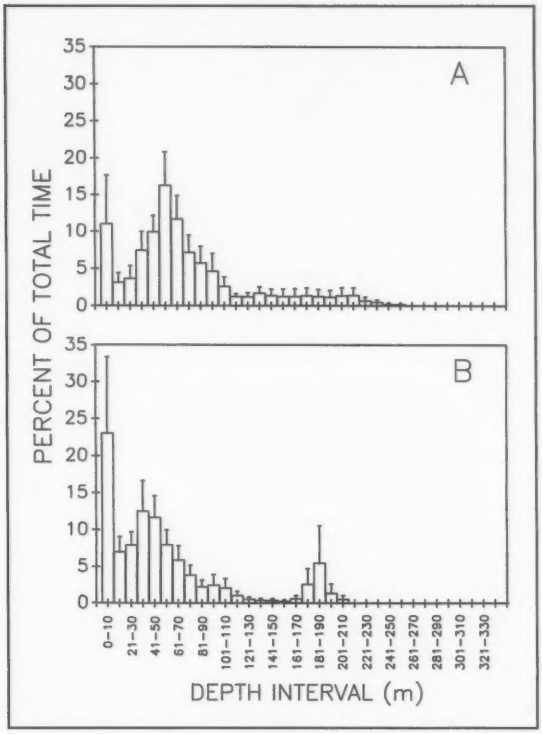


**Figure 11**
Yellowfin tuna daytime distribution (A) shows two modes, one at the surface and one between 60 and 90 m, which corresponds to the normal position of the interface between the mixed layer and the top layers of the thermocline. Nighttime distribution (B) reflects the tendency of these fish to swim closer to the surface at night. In this and subsequent histograms, bars = standard error.

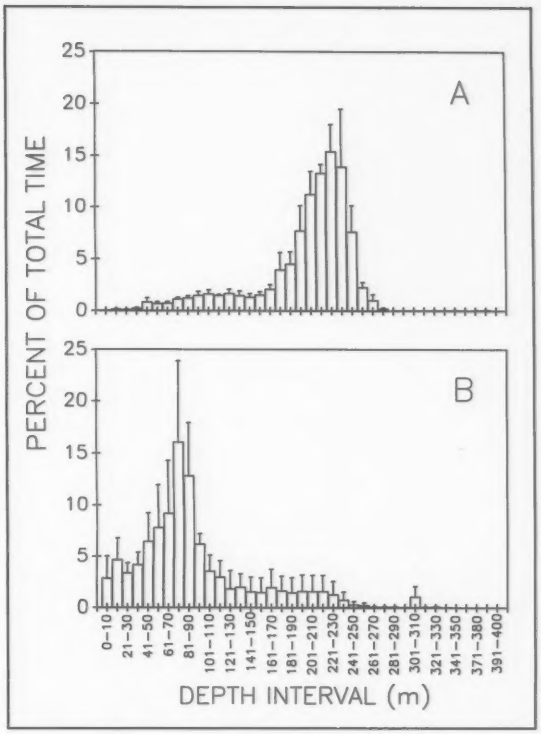


**Figure 12**
Daytime distribution of bigeye tuna (A) displays a major mode between 200 and 240 m, whereas nighttime distribution is much shallower (B), with the predominant distribution falling between 70 and 90 m.

The tendency of FADs to bring fish closer to the surface was even more apparent in the deeper-swimming bigeye tuna, as was dramatically demonstrated by BE8603 which stayed close to S FAD for 6 hours of daylight before moving away at midday. Figure 13 illustrates the rapid change of depth that coincided with

**Figure 13**
Plot of the on-FAD and off-FAD movements of bigeye tuna BE8603. Arrow indicates when fish departed R FAD.

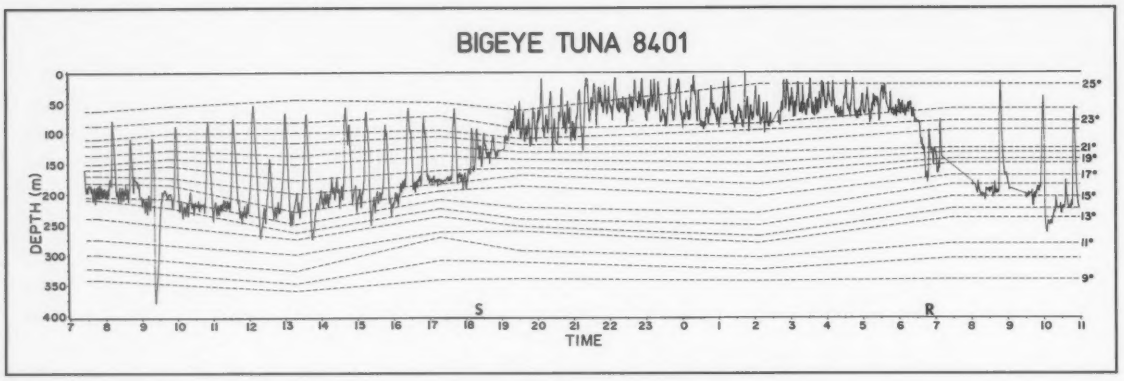


**Figure 14**
Plot of day-night-day movements of bigeye tuna BE8401. The rapid dive shown in Figure 9 can be seen at 0915 on the first day.

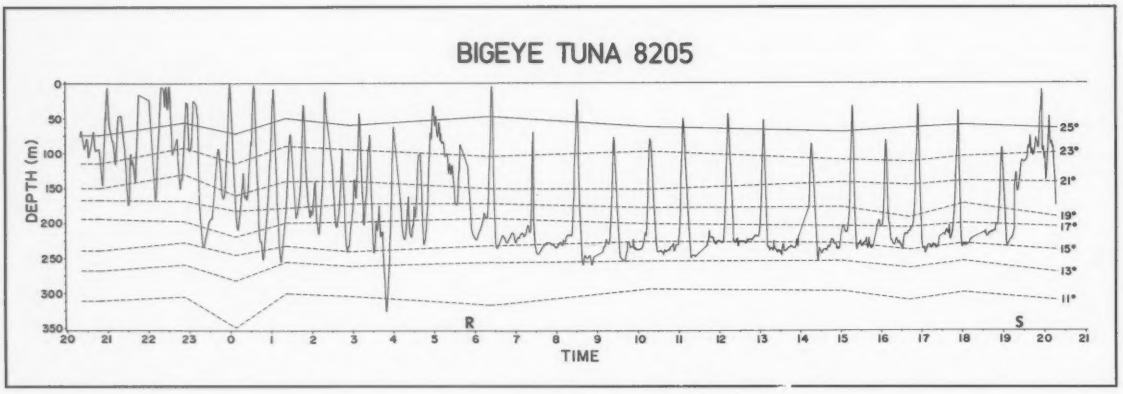


**Figure 15**
Plot of vertical movements of bigeye tuna BE8205 showing extremely regular daytime upward excursions. These excursions consistently terminated in the zone encompassing the interface between the mixed layer and the thermocline.

the departure of this fish from the FAD. The subsequent depth and pattern of swimming were similar to those shown by the other bigeye tuna that departed their respective FADs almost immediately upon release (Figs. 14, 15). Bigeye tuna BE8706, which remained within 200 m of S FAD for 27.0 hours of the 30.0-hour track, displayed a predominant on-FAD daytime depth of between 50 and 60 m, whereas the predominant, pooled, daytime off-FAD depth of the other three bigeye tuna was 230 m.

### Temperature distribution

For the yellowfin tuna, the surface mixed layer (ML) and first degree of the thermocline (ML-1) accounted for 68% of daytime distribution (Fig. 16A). After sunset, the mixed layer alone represented over 62% of the distribution of this species, with the upper 2 degrees of the thermocline contributing an additional 26% of the yellowfin tuna's nighttime distribution (Fig. 16B). Obviously, the warmer nighttime distributions are reflective of the generally shallower depths occupied during the hours of darkness.

In the case of the bigeye tuna, daytime distribution was more dependent on absolute temperature than temperature relative to the surface mixed layer. Thus, in daytime 62.5% of the pooled off-FAD distribution occurred between 14° and 17°C (Fig. 17A). On an individual basis, the strong influence of temperature on daytime vertical distribution was demonstrated by fish BE8401 which consistently oscillated between the 15° and 17°C isotherms even though these isotherms were changing in depth over the course of the track (Fig. 14). Of this bigeye tuna's daytime movements, 68%

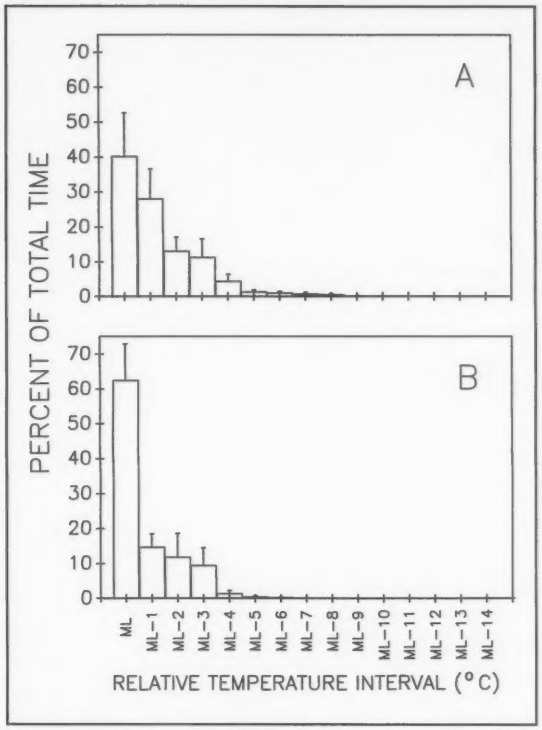


**Figure 16**
Yellowfin tuna temperature distributions relative to the upper mixed layer (ML). (A) day, (B) night.

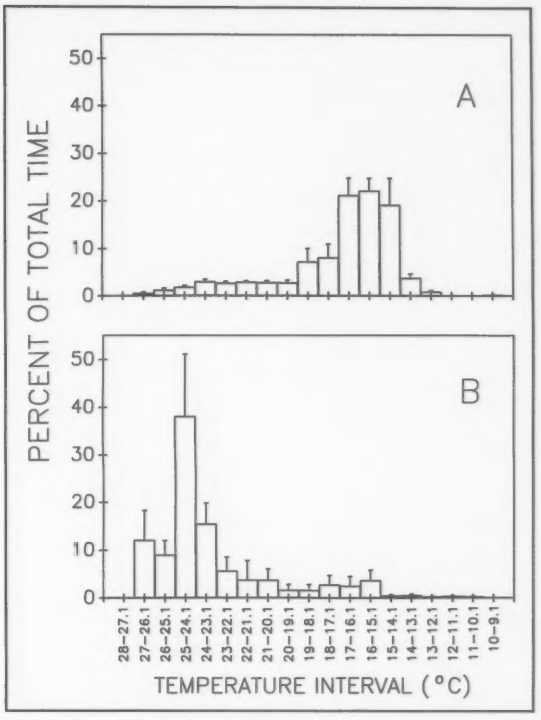


**Figure 17**
Bigeye tuna temperature distribution. (A) day, (B) night.

occurred between 14° and 17°C. Similarly, BE8205 spent 70% of daylight hours between the 14° and 16°C isotherms (Fig. 15), and BE8603 spent 76% of off-FAD daylight hours between 14° and 17°C isotherms (Fig. 13).

As with the yellowfin, bigeye tuna occupied warmer waters at night (Fig. 17B). The difference between daytime and nighttime temperature distributions was greater for bigeye than for yellowfin tuna because of the much deeper and colder daytime distribution of the bigeye tuna and their comparatively large nocturnal upward shift.

Regular, large, upward excursions were a major feature of the daytime swimming behavior of all the bigeye tuna that were tracked in off-FAD situations (Figs. 13, 14, and 15). This behavior occurred regardless of the type of horizontal movement (e.g., meandering versus straight line). These excursions were comprised of rapid ascents and descents of uniform rate. Ascents usually peaked close to the bottom of the mixed layer and the descending phases usually terminated at the predominant daytime swimming depth. These regular excursions did not occur at night or when on-FAD. For example, these upward excursions were exhibited by fish BE8603 only after it departed S FAD and assumed a deeper off-FAD distribution (Fig. 13). The periodicity and duration of these large excursions were quite regular. For instance, 13 daytime peaks exhibited by BE8205 had a peak-to-peak interval of 57.7 minutes (±7.0 SD) and a duration of 12.0 minutes (±2.6 SD).

Individual fish of both species tended to adopt consistent upper and lower limits to their movements such that, even if they were making frequent upward and downward movements, these were often terminated at consistent depths or temperatures. The most common of these turnaround points was the zone encompassing the bottom of the surface mixed layer and the uppermost layers of the thermocline. Thus, in the case of yellowfin YF8305, the top of the thermocline represented the bottom of dives made from the surface and the starting and finishing points of dives made to deeper depths, most of which had a consistent "floor" around the 20°C isotherm at approximately 130 m (Fig. 10). Similarly, in addition to the well-defined temperature confines of their smaller vertical oscillations, most

of the bigeye tunas' large upward excursions consistently terminated near the interface between the thermocline and the mixed layer (Figs. 13, 14, and 15).

Examples of possible fly-glide behavior (Weihs 1973, Carey and Olsen 1982) were observed in tracks of yellowfin and bigeye tuna, a very consistent example being BE8401, which exhibited "sawtooth" oscillations with a period of approximately 4 minutes and an amplitude between 35 and 45 m for the entire 11-hour daylight segment of the track. Similar, persistent oscillating daytime behavior was exhibited by fish YF8506 as it moved on a direct course away from S FAD (Fig. 18). For instance, between 0930 and 1815 this fish swam on a straight southwesterly course at an apparently constant horizontal speed of 1.02 m/second (Fig. 5). Assuming this constant speed, the descending angles during this period averaged 6.06° (±0.7 SD, $N = 11$), and the climbing angles averaged 9.55° (±1.4 SD, $N = 11$) with 100% of the climbing angles being greater than the descending angles. Also, of the measurable oscillations occurring between 0915 and 1815, 39 out of 46 (85%) displayed longer falling than rising phases, suggesting active upward swimming followed by a comparatively passive downward glide. These oscillations were characterized by constant rates of ascent and descent, with abrupt changes in direction linking the falling and rising phases (Fig. 18).

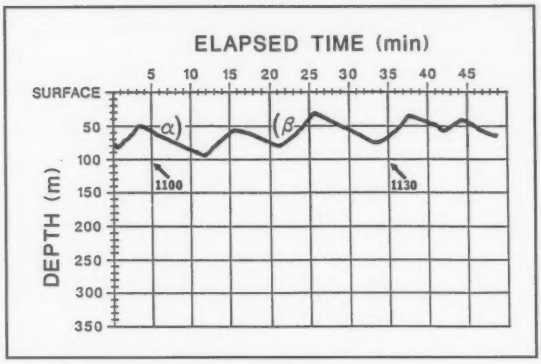


**Figure 18**

Yellowfin tuna YF8506 showed oscillations suggestive of "fly-glide" behavior while moving on an essentially straight course away from S FAD (cf. Fig. 5). All descending angles ($\alpha$) were smaller than the climbing angles ($\beta$).

## Discussion

Using two tie wraps appears to be a satisfactory way of attaching transmitters to tunas. Transmitters attached in this way were carried successfully by four captive fish for several weeks, and one of the tracked fish was caught in good health (and still carrying the transmitter) by a fisherman 2 weeks after we terminated the track. The similarity of vertical and horizontal movements across tracks also suggests minimal alteration of normal behavior.

The association of these tuna with a daytime range, whether FAD or reef perimeter, was extremely strong. In the case of FADs, several fish spent many hours within a few meters of the mooring line. Similarly, none of the reef-associated fish made significant offshore movements during daylight hours. In fact, the alongshore movements were remarkable for their fidelity to the outer reef contour. Combining FAD-associated and reef-perimeter fish, 10 of the 15 fish tracked in this study moved within a well-defined home range during daylight hours and two other fish were lost before any diel patterns could be observed. Most of the fish made nocturnal excursions away from their respective daytime habitats. Similar, consistent diurnal behavior has been previously observed in a 44-cm skipjack tuna, which returned to the same reef after making offshore excursions on each of six nights that it was tracked (Yuen 1970).

This skipjack tuna and the yellowfin tuna tracked in the present study represent the smaller size classes of these species. For fish of these sizes, the reef dropoff probably represents a zone of enhanced prey density where epipelagic species, such as bigeye scad *Decapturus crumenopthalmus*, mackerel scad *D. pinnulatus*, and flying fish (Exocidae), can be found in proximity to reef species which are also prey for these tunas (Hida 1973). The nighttime excursions away from the island reefs and FADs may be foraging behavior targeting on squid and shrimp, which come up from greater daytime depths and which are important components of yellowfin tuna diets (Reintjes and King 1953, King and Ikehara 1956, Brock 1985). Even though the reef-associated fish moved out into deeper water, the nighttime distribution of these yellowfin tuna was closer to the surface than their daytime depths.

The strong daytime association of yellowfin tuna with the FADs, and their nighttime excursions away from them, appears to be analogous to the behavior of island-associated fish patroling the outer reef dropoff. That is, yellowfin tuna appear to respond to FADs as outliers of the natural island topography (e.g., as offshore pinnacles). However, the FAD-associated fish may be paying an energetics penalty because the forage resource at FADs is probably considerably smaller than that available at the reef perimeter. This is indicated by the fact that yellowfin tuna caught at FAD locations have significantly smaller volumes of food in their guts and a significantly higher frequency of completely empty stomachs than do fish caught away from FADs (Brock

1985). Alternatively, it is possible that nighttime feeding excursions away from the FADs, combined with the apparently reduced daytime swimming activity at FADs as compared with reef banks, result in an energetics balance equivalent to that of better-fed, but more active, open-ocean fish or reef-perimeter fish. Even though feeding may not occur as often at FADs as in other areas, FAD-associated tuna may conserve energy normally associated with active hunting. By orienting to FADs, the fish maintain a fixed position in the current flow and may feed on current-borne prey, a situation analogous to trout holding station in a river. The predominant upcurrent orientation of FAD-associated tunas may serve to intercept incoming prey items before they can use the FAD structure for shelter. These feeding advantages would not pertain to tuna associated with logs, which drift with the current and cannot provide the function of serving as a fixed point in a stream. Thus, although logs may indicate areas of enriched forage for planktivores by marking zones of Langmuir cell convergence (Fedoryako 1982), they are unlikely to supply the high food demands of even a medium-sized school of tuna, and, in fact, small fishes found in association with logs are not an important part of the diets of tuna taken from beneath logs (Hunter and Mitchell 1967).

There are other indications that different phenomena may underlie the association of tuna with natural debris and their association with FADs. For instance, fishing techniques which take advantage of log-associated tuna indicate that in these circumstances the tuna tend to aggregate around logs at night and move away in the daytime—exactly the opposite of the behavior observed in the current study. However, in the log situations, tuna behavior may be perturbed by the use of lights placed on the logs by fishermen. Also, since tunas probably are capable of magneticaly mediated orientation (Walker 1984), and in our own study exhibited precise feats of navigation (e.g., returning to the same FAD; navigating between FADs; maintaining straight azimuths over prolonged periods of time), it is unlikely that tunas have trouble distinguishing between logs and FADs because, unlike logs, FADs are both stationary and attached to the ocean floor by visibly (and possibly, acoustically) discernible chain and rope.

The combined data yield an average nightime excursion distance of approximately 5 nmi. This would indicate that to maximize the ability of FADs to aggregate yellowfin tuna consistently, and to minimize the influence of FADs on coastline-associated populations, FADs should be placed a minimum of 5 nmi from the nearest 40-fathom bank. This interpretation is supported by the track of fish YF8504 which rapidly traversed the 3.5 nmi to the 40-fathom contour when disturbed at R FAD by a school of porpoises. Similarly, YF8405 was caught at R FAD 2 weeks after being tracked along the adjacent coastline which, at its nearest point, is between 3.5 and 4.0 nmi away. In fact, optimal FAD placement would be greater than 10 nmi offshore (or from the nearest 40-fathom bank) so that the radii of influence of the FAD and the coastline do not overlap. Frequent anecdotal observations and the impressions of Hawaiian fishermen suggest that FADs located 10 nmi offshore are more consistently productive than FADs located closer to shore.

Daytime orientation of yellowfin tuna to the top layers of the thermocline, with excursions into the mixed layer and to the surface, and a nighttime shallowing into the mixed layer, are consistent with patterns observed by Yonemori (1982) and Carey and Olson (1982). The yellowfin tuna in the current study displayed a particularly strong adherence to the interface between the surface mixed layer and the thermocline when exhibiting straight-line movements. Similar behavior has been previously noted by Carey and Olson (1982). In the present study, these "traveling" fish would often abruptly alternate between the surface and the thermocline interface, both of which might serve to assist straight-line orientation in what is otherwise a truly three-dimensional habitat. By contrast, fish orienting around FADs showed either little vertical movement or vertical movements that were sinusoidal and largely within the mixed layer.

The depth and temperature distributions derived from the bigeye tuna tracks are in good agreement with distributional data obtained by analysis of longline fishing success (Saito 1975; Hanamoto 1976, 1987). These fishery data indicate maximum abundance at depths >200 m and in temperatures between 11° and 15°C, where the dissolved oxygen is >1 mL/L. However, the tracking data suggest daytime distribution (220–240 m, 14–17°C) is influenced at least as much by temperature as by depth, and none of the catch-rate studies indicate the dramatic nighttime upward shift that the tracking data reveal.

The average sustained swimming speed derived from the straight sections of the current yellowfin tuna tracks was 4.46 Km/hour (range 3.2–6.5 Km/hour, Table 1), which is similar to the 4.27 Km/hour average (range 2.4–7.8 Km/hour) reported by Carey and Olson (1982) for fish having an average fork length 41% greater than those used in our study. This comparison would suggest that absolute traveling (sustainable) swimming speed for this species does not increase with size, at least for fish between 45 and 100 cm FL. This constancy of swimming speed, regardless of increasing fish length, is consistent with the model generated by Magnuson (1973, 1978), which predicts that increased weight associated with increasing length is

offset in this species by the allometric growth of the swim bladder, thereby precluding the need to increase hydrodynamic lift through higher swimming speeds. However, the sustained swimming speeds observed during these tracks (average of 1.24 m/second) are considerably higher than the 0.5 to 0.6 m/second predicted by Magnuson (1978) for fish of this size. Obviously, field observations of larger fish would be useful in further testing the Magnuson model.

Periods of possible fly-glide behavior were observed in sections of tracks of yellowfin and bigeye tunas. These oscillations, which in one instance (YF8506) were exhibited for the entire daylight portion of a straight azimuth track, have been hypothesized to result in a saving of energy required for locomotion between two points (Weihs 1973, Magnuson 1978). As predicted by this model, most gliding phases lasted longer than the ascending phases, and the descending and ascending legs were connected by abrupt angles, which maximize energy transfer from the gliding to the flying phase. Thus, using the "fly" angle ($\beta$) of 9.55 and "glide" angle ($\alpha$) of 6.06 obtained from YF8506, and a swim/glide drag ratio ($k$) of 1.2 (Magnuson 1978), the equation:

$$\text{Energy saving} = 1 - \frac{\tan \alpha}{\sin \beta + (\tan \alpha \cdot \cos \beta)} \times \left(1 + \frac{1 \sin \beta}{k \sin \alpha}\right)$$

results in an energy saving of 9.4% compared with level swimming over the same distance. And, where $T$ is the increased time to travel the same distance using a fly/glide strategy as opposed to level swimming, using the equation

$$T = \frac{\sin \alpha + \sin \beta}{\sin (\alpha + \beta)}$$

indicates that this strategy results in only a 0.9% increase in time to travel the same distance.

The extremely regular, large, upward excursions made by all the off-FAD bigeye tuna during daylight hours may represent behavioral thermoregulation. At the low (14–17°C) ambient temperatures adopted by these fish, their core temperatures possibly drop below some threshold level which requires movement into warmer water to regain optimum body temperatures. If this is the case, it would suggest that there exists a strong motivation for inhabiting the deep cold layers observed during these tracks. A possible motivation would be the opportunity to feed on deepwater fish, squid, and crustaceans which the bigeye tuna then follow into shallower depths at night when these prey organisms migrate toward the surface. Monitoring the core muscle temperatures of bigeye tuna would indicate if, in fact, the large upward excursions are a form of behavioral thermoregulation which, when combined with physiological thermoconservation, allows these fish to exploit an otherwise unreachable resource.

## Acknowledgments

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# Food Habits of California Sea Lions *Zalophus californianus* at San Clemente Island, California, 1981–86

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**Abstract.**– We studied the food habits of the California sea lion *Zalophus californianus* at San Clemente Island, California, from September 1981 through September 1986 using fish otoliths, cephalopod beaks, and other prey remains we recovered from 1476 fecal samples (i.e., scats). We identified 44 types of prey to species and 8 types of prey to genus. Seven types of prey occurred in at least 10% of scats: northern anchovy *Engraulis mordax* (51.3%); jack mackerel *Trachurus symmetricus* (24.6%); pelagic red crab *Pleuroncodes planipes* (21.2%); Pacific whiting *Merluccius productus* (19.6%); rockfishes, *Sebastes* spp. (19.0%); market squid *Loligo opalescens* (16.3%); and blacksmith *Chromis punctipinnis* (10.7%). We examined trends in the occurrence of these seven species and of Pacific mackerel *Scomber japonicus* and octopus (*Octopus* spp.) in scats of California sea lions. We found significant differences among seasons and years, and season-year differences in the occurrence of northern anchovy, jack mackerel, Pacific whiting, and octopus ($P \leq 0.01$). Significant effects due to year and season-year interaction were found for pelagic red crab, rockfish, market squid, and blacksmith. Pacific mackerel showed a significant difference only among years. Significant differences in the occurrence of Pacific whiting, northern anchovy, jack mackerel, Pacific mackerel, market squid, octopus, and pelagic red crab ($P < 0.01$) were found during pre-El Niño, El Niño, and post-El Niño periods.

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Knowledge of California sea lion *Zalophus californianus* food habits in the Southern California Bight (SCB, Fig. 1) has come from stomach content analysis by Scheffer and Neff (1948), and Fiscus and Baines (1966); and from the 1978–79 spring and summer study at San Miguel Island from scat (i.e., fecal) analysis by Antonelis et al. (1984). These studies identified a wide variety of prey. Antonelis et al. (1984) reported that Pacific whiting, market squid, juvenile rockfish, and northern anchovy were the four most important prey at San Miguel Island. A 4-year study at the Farallon Islands in northern California (outside the breeding area) found that sea lions switched between Pacific whiting and juvenile rockfish (Bailey and Ainley 1982).

From 1981 to 1986, we examined prey consumed by California sea lions using the shoreline located at and south of Mail Point, San Clemente Island (SCI, Fig. 1). San Clemente Island has one of the smallest rookeries in the SCB (producing approximately 666 pups in 1981) as compared with San Miguel and San Nicolas islands (producing approximately 8255 and 6704 pups, respectively, in 1981; DeMaster et al. 1982, Stewart and Yochem 1984, Oliver and Lowry 1987). We analyzed fecal samples (scats) to identify prey composition and temporal changes in the diet. This period was characterized by an abnormal influx of warm water into the SCB during the 1982–83 El Niño/Southern Oscillation (McGowan 1984). Effects of this El Niño within the SCB became evident in October 1982, when sea-surface temperatures were 1–2°C above normal, and zooplankton levels declined (McGowan 1984). Water temperatures returned to normal in October–November 1984 (F. Miller, Inter-Am. Trop. Tuna Comm., La Jolla, CA 92038, pers. commun., Oct. 1986). This warm-water period off California has been referred to as the California El Niño (McGowan 1984, Fiedler et al. 1986).

## Methods

### Sample collection

We collected fresh and dry scats during 40 trips to SCI with between-trip intervals ranging from 2 weeks to 3 months. Scats were separated into one of three categories: (1) fresh

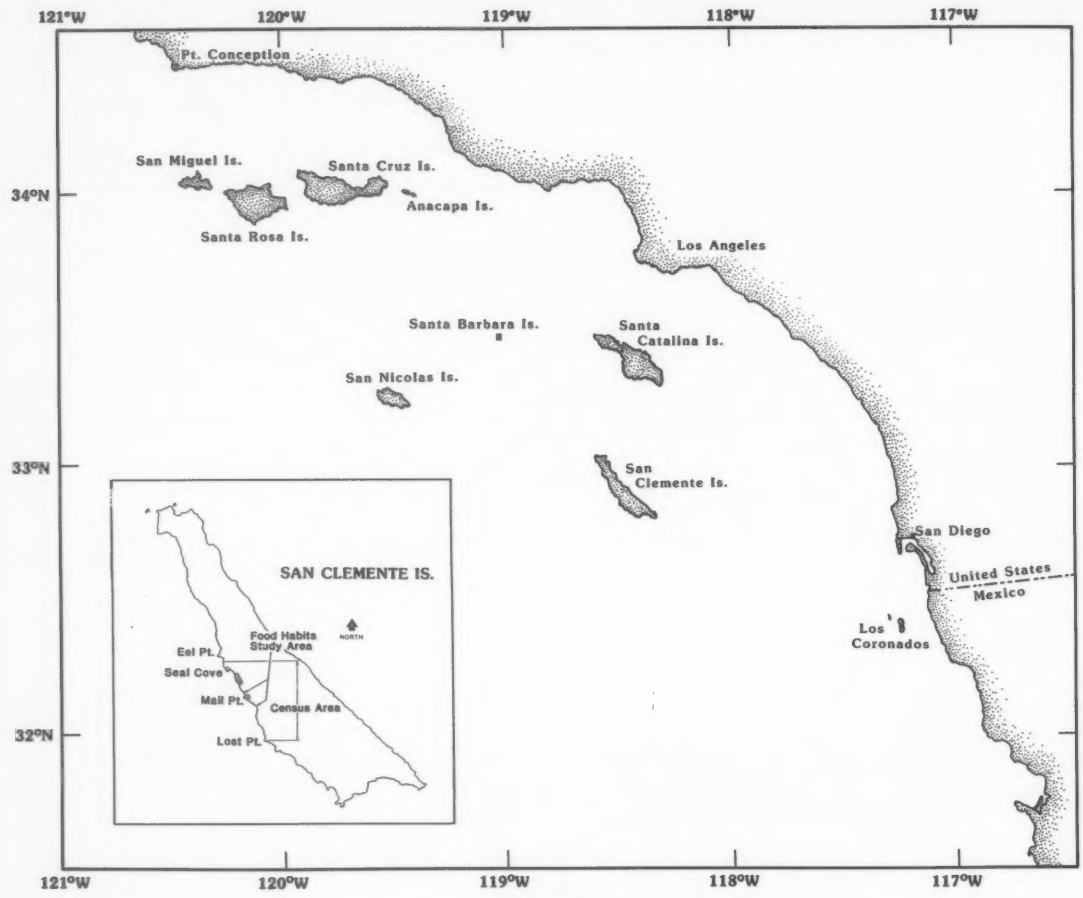



**Figure 1**
Map showing Southern California Bight (SCB) and San Clemente Island (SCI).

scats, (2) dried scats representing one between-trip interval, and (3) dried scats representing more than one between-trip interval. Fresh scat samples represented the diet of sea lions within 3 to 4 days of the collection. The second category provided dietary information from the previous scat collection period to the time represented by fresh scats. The third category represented a much longer period.

Each scat was placed in a plastic bag, stored in an air-tight plastic container, and frozen until processed. Scats were soaked in a mild soap solution for 1–5 days, and then rinsed with water through two or three nested sieves. During September 1981–March 1983 we used three sieves (mesh sizes 2.8 mm, 1.5 mm, and 1.00 mm) and during April 1983–September 1986 we used two sieves (mesh sizes 2.8 mm and 0.710 mm). After rinsing, we collected fish otoliths, cephalopod beaks, shark teeth, and cartilaginous vertebrae. Otoliths, shark teeth, and cartilaginous vertebrae were air dried and stored in gelatin capsules; cephalopod beaks were stored in vials containing 70% ethanol. We noted the presence or absence of fragments of pelagic red crabs *Pleuroncodes planipes*.

## Sample analysis

Prey items were identified to the lowest taxon possible from comparative specimens and drawings (Iverson and Pinkas 1971, Eschmeyer et al. 1983). We used sagittal otoliths to identify teleost fishes, cephalopod beaks to identify squid and octopus, teeth to identify elasmobranchs, and exoskeletal fragments to identify pelagic red crabs. We counted left and right sagittal otoliths, and upper and lower cephalopod beaks.

**Table 1**
California sea lion *Zalophus californianus* scat samples collected seasonally from San Clemente Island, California, 1981–86.

| Year | Season | Number of collection trips | Number of scats collected | | | |
|---|---|---|---|---|---|---|
| | | | | Dry | | |
| | | | Fresh | 1 between-trip interval | >1 between-trip interval | Total collected |
| 1981 | Autumn | 3 | 22 | 19 | 7 | 48 |
| 1981–82 | Winter | 1 | 0 | 3 | 0 | 3 |
| 1982 | Spring | 4 | 27 | 80 | 52 | 159 |
| 1982 | Summer | 4 | 76 | 67 | 7 | 150 |
| 1982 | Autumn | 1 | 1 | 53 | 0 | 54 |
| 1982–83 | Winter | 2 | 3 | 56 | 0 | 59 |
| 1983 | Spring | 3 | 37 | 73 | 60 | 170 |
| 1983 | Summer | 2 | 6 | 71 | 10 | 87 |
| 1983 | Autumn | 1 | 22 | 56 | 17 | 95 |
| 1983–84 | Winter | 3 | 93 | 51 | 4 | 148 |
| 1984 | Spring | 2 | 81 | 20 | 16 | 117 |
| 1984 | Summer | 3 | 88 | 1 | 0 | 89 |
| 1984 | Autumn | 2 | 13 | 40 | 0 | 53 |
| 1984–85 | Winter | 1 | 0 | 16 | 0 | 16 |
| 1985 | Spring | 1 | 11 | 1 | 0 | 12 |
| 1985 | Summer | 2 | 60 | 0 | 0 | 60 |
| 1985 | Autumn | 1 | 25 | 0 | 0 | 25 |
| 1986 | Spring | 1 | 44 | 0 | 0 | 44 |
| 1986 | Summer | 2 | 65 | 0 | 0 | 65 |
| 1986 | Autumn | 1 | 22 | 0 | 0 | 22 |
| Total | | 40 | 696 | 607 | 173 | 1476 |

We used indices of occurrence, composition, and number to quantify prey taxon consumed by sea lions. Only scat samples containing otoliths, cephalopod beaks, shark teeth, cartilaginous vertebrae, or pelagic red crab fragments were used in the analysis. The occurrence index, or percent occurrence (PO), is a measure of the percentage of scat samples in which a prey taxon occurred. The composition index, or percent prey composition (PPC), is a measure of the percentage of occurrences for each prey taxon from a tally of occurrences from all prey taxa found in a group of samples. The number index, or percent minimum number (PMN), measures the percentage of numbers of individual prey taxon. To compute the number index, we used the maximum count of either left or right otoliths, or upper or lower beaks, which represent the minimum number of individual prey taxon. The counts for all prey taxa are summed and the percentage of each prey taxon is determined from the sum of all counts. The number index is, then, the percentage represented by each prey taxon from the sum of all maximum counts taken of all prey taxa found in a group of samples.

Interpretation of the number index is limited because it excludes (1) all prey hard parts found that were broken or digested, and not categorized as either left or right otoliths or upper or lower beaks, and (2) prey that lacked otoliths or beaks (e.g., pelagic red crabs and sharks). However, we think that this index is useful because fish and cephalopods represented the majority of prey in scat samples.

Percent occurrence indicates prey consumption without regard to other prey, and may indicate temporal availability, selectivity, or ease of capture of individual prey. Percent prey composition indicates the relative proportions of prey consumed. Percent minimum number of prey indicates numbers of prey consumed and is an index of the rate of consumption of individual prey.

## Statistical analysis

We used all scats to determine what prey taxa were consumed, and then limited our examination of temporal variations in prey consumption to prey that occurred in at least 10% of these scats, were found in at least 80% of the seasons, or were occasionally very abundant. Only fresh scats and dried scats representing one between-trip interval were used in the temporal analyses of sea lion diets. We combined the 40 collection trips (Table 1) by season into winter (December–

## Table 2

Number of prey occurrences (*n* Occur), percent occurrence (PO), percent prey composition (PPC), minimum number of individual prey (*n* Ind.), and percent minimum number (PMN) of prey found in 1309 California sea lion scats collected at San Clemente Island, California, 1981–86.

| Prey | | | | | | |
|---|---|---|---|---|---|---|
| Scientific name | Common name | *n* Occur | PO | PPC | *n* Ind. | PMN |
| *Engraulis mordax* | northern anchovy | 672 | 51.3 | 24.7 | 9,398 | 54.4 |
| *Trachurus symmetricus* | jack mackerel | 322 | 24.6 | 11.8 | 1,220 | 7.1 |
| *Pleuroncodes planipes** | pelagic red crab | 277 | 21.2 | 10.2 | —** | — |
| *Merluccius productus* | Pacific whiting | 256 | 19.6 | 9.4 | 2,110 | 12.2 |
| *Sebastes* spp. | rockfish | 249 | 19.0 | 9.2 | 1,245 | 7.2 |
| *Loligo opalescens* | market squid | 214 | 16.3 | 7.9 | 1,516 | 8.8 |
| *Chromis punctipinnis** | blacksmith | 140 | 10.7 | 5.1 | 580 | 3.4 |
| *Scomber japonicus* | Pacific mackerel | 125 | 9.5 | 4.6 | 215 | 1.2 |
| *Octopus* spp. | octopus | 67 | 5.1 | 2.5 | 523 | 3.0 |
| *Onychoteuthis borealijaponicus* | squid | 39 | 2.2 | 1.1 | 33 | <0.5 |
| *Lyopsetta exilis* | slender sole | 11 | 0.8 | <0.5 | 19 | <0.5 |
| *Oxyjulis californica** | señorita | 14 | 1.1 | 0.5 | 20 | <0.5 |
| *Porichthys notatus* | plainfin midshipman | 9 | 0.7 | <0.5 | 11 | <0.5 |
| *Abraliopsis* spp.* | squid | 9 | 0.7 | <0.5 | 11 | <0.5 |
| *Gonatus* spp. | squid | 9 | 0.7 | <0.5 | 11 | <0.5 |
| *Lycodes cortezianus** | bigfin eelpout | 7 | 0.5 | <0.5 | 8 | <0.5 |
| *Sebastolobus alascanus** | shortspine thornyhead | 6 | 0.5 | <0.5 | 7 | <0.5 |
| *Microstomus pacificus* | dover sole | 6 | 0.5 | <0.5 | 8 | <0.5 |
| *Glyptocephalus zachirus* | rex sole | 6 | 0.5 | <0.5 | 7 | <0.5 |
| *Icichthys lockingtoni* | medusafish | 5 | <0.5 | <0.5 | 7 | <0.5 |
| *Xeneretmus ritteri** | stripefin poacher | 3 | <0.5 | <0.5 | 5 | <0.5 |
| *Citharichthys sordidus* | Pacific sanddab | 4 | <0.5 | <0.5 | 5 | <0.5 |
| *Atherinops affinis** | topsmelt | 3 | <0.5 | <0.5 | 4 | <0.5 |
| *Semicossyphus pulcher** | sheephead | 3 | <0.5 | <0.5 | 3 | <0.5 |
| *Seriphus politus* | queenfish | 2 | <0.5 | <0.5 | 26 | <0.5 |
| *Cypselurus californicus** | California flying fish | 2 | <0.5 | <0.5 | 8 | <0.5 |
| *Genyonemus lineatus* | white croaker | 2 | <0.5 | <0.5 | 6 | <0.5 |
| *Galeorhinus zyopterus** | soupfin shark | 2 | <0.5 | <0.5 | — | — |
| *Symbolophorus californiensis* | California lanternfish | 2 | <0.5 | <0.5 | 2 | <0.5 |
| *Paralabrax clathratus** | kelp bass | 2 | <0.5 | <0.5 | 2 | <0.5 |
| *Chilara taylori* | spotted cusk-eel | 2 | <0.5 | <0.5 | 2 | <0.5 |
| *Cymmatogaster aggregata* | shiner surfperch | 2 | <0.5 | <0.5 | 2 | <0.5 |
| *Stenobrachius leucopsarus* | northern lampfish | 2 | <0.5 | <0.5 | 2 | <0.5 |
| *Paralabrax* sp.* | seabass | 1 | <0.5 | <0.5 | 3 | <0.5 |
| *Ocythoe tuberculata** | squid | 1 | <0.5 | <0.5 | 2 | <0.5 |
| *Girella nigricans* | opaleye | 1 | <0.5 | <0.5 | 2 | <0.5 |
| *Zalembius rosaceus* | pink surfperch | 1 | <0.5 | <0.5 | 1 | <0.5 |
| *Zaniolepis* sp.* | combfish | 1 | <0.5 | <0.5 | 1 | <0.5 |
| *Xeneretmus* sp.* | poacher | 1 | <0.5 | <0.5 | 1 | <0.5 |
| *Prionace glauca** | blue shark | 1 | <0.5 | <0.5 | — | — |
| *Argentina sialis** | Pacific argentine | 1 | <0.5 | <0.5 | 1 | <0.5 |
| *Hippoglossina stomata** | bigmouth sole | 1 | <0.5 | <0.5 | 1 | <0.5 |
| *Parophrys vetulus* | english sole | 1 | <0.5 | <0.5 | 1 | <0.5 |
| *Xeneretmus triacanthus** | bluespotted poacher | 1 | <0.5 | <0.5 | 1 | <0.5 |
| *Ceratoscopelus townsendi** | dogtooth lampfish | 1 | <0.5 | <0.5 | 4 | <0.5 |
| *Citharichthys* sp. | sanddab | 1 | <0.5 | <0.5 | 1 | <0.5 |
| *Careproctus melanurus** | blacktail snailfish | 1 | <0.5 | <0.5 | 1 | <0.5 |
| *Medialuna californiensis** | halfmoon | 1 | <0.5 | <0.5 | 3 | <0.5 |
| *Synodus lucioceps** | California lizardfish | 1 | <0.5 | <0.5 | 1 | <0.5 |
| *Octopoteuthis deletron** | squid | 1 | <0.5 | <0.5 | 1 | <0.5 |
| Unid. Myctophidae | lanternfish | 17 | 1.3 | 0.6 | 29 | <0.5 |
| Unid. Embiotocidae | surfperch | 4 | <0.5 | <0.5 | 7 | <0.5 |
| Unid. Atherinidae | silverside | 3 | <0.5 | <0.5 | 3 | <0.5 |
| Unid. Labridae | wrasse | 3 | <0.5 | <0.5 | 8 | <0.5 |
| Unid. Cottidae | sculpin | 2 | <0.5 | <0.5 | 2 | <0.5 |
| Unid. Zoarcidae | eelpout | 2 | <0.5 | <0.5 | 2 | <0.5 |

**Table 2 (continued)**

| Prey | | | | | | |
|---|---|---|---|---|---|---|
| Scientific name | Common name | *n* Occur | PO | PPC | *n* Ind. | PMN |
| Unid. Gonatidae | squid | 1 | <0.5 | <0.5 | 1 | <0.5 |
| Unid. Scombridae | mackerel or tuna | 1 | <0.5 | <0.5 | 2 | <0.5 |
| | Unid. flatfish | 5 | <0.5 | <0.5 | 6 | <0.5 |
| | Unid. cephalopod | 31 | 2.4 | 1.1 | 19 | <0.5 |
| | Unid. cartilaginous fish | 2 | <0.5 | <0.5 | — | — |
| | Unid. fishes | 83 | 6.3 | 3.1 | 62 | <0.5 |

*Not previously reported as prey of California sea lions.
**Data impossible to compute in fields marked with a dash (—).

February), spring (March–May), summer (June–August), and autumn (September–November). We also categorized our sample into three groups related to the California El Niño: (1) pre-El Niño (September 1981–August 1982), (2) El Niño (November 1982–September 1984), and (3) post-El Niño (November 1984–September 1986).

We tested for seasonal and yearly differences in presence or absence of each prey taxon using two-way ANOVA (Program 7D of BMDP-87; Dixon 1985) in the binomial format. Two data sets were identified with full cells in order to meet the requirements of the test: (1) all seasons for the years 1982–85 (called four-season-four-year data set); and (2) three seasons (spring, summer, and autumn) for 1982–86 (called three-season-five-year data set). We identified prey taxa that showed significant season, year, and season-year interaction differences in their occurrence through time using Browne-Forsythe analysis of variance for unequal variances. For the pre-El Niño, El Niño, and post-El Niño comparisons, we tested for differences in presence or absence of the same nine prey taxa using two-way Browne-Forsythe ANOVA (Dixon 1985) in the binomial format.

We also examined temporal differences in the relative number of different prey taxa found per scat (1, 2, 3, 4, 5, or >5). Pearson's chi-square test (Dixon 1985) was used to test for differences among numbers of prey occurring per scat.

## Results

### Identification of prey remains

In the 1476 scats collected (Table 1), we found the following: (1) 1455 scats (98.5%) contained fish remains (i.e., bones, otoliths, or eye lenses); (2) 525 scats (35.5%) contained cephalopod remains (i.e., beaks or eye lenses); (3) 1309 scats (88.6%) contained fish otoliths, cephalopod beaks, or other prey remains that were used to identify prey; (4) 1271 scats (86.1%) contained fish otoliths; and (5) 344 scats (23.3%) contained cephalopod beaks.

We identified 95.4% of 2647 prey occurrences to species, genus, or family (Table 2). Of the 2,647 prey occurrences, 75.2% were bony fishes, 14.1% were cephalopod, 10.5% were crustacea (99.3% of crustacea were pelagic red crab), and 0.2% were cartilaginous fish. We identified 44 prey taxa to species level and 8 to genus level. Seven prey taxa occurred in >10% of scats: northern anchovy *Engraulis mordax* (51.3%); jack mackerel *Trachurus symmetricus* (24.6%); pelagic red crab *Pleuroncodes planipes* (21.2%); Pacific whiting *Merluccius productus* (19.6%); rockfishes, *Sebastes* spp. (19.0%); market squid *Loligo opalescens* (16.3%); and blacksmith *Chromis punctipinnis* (10.7%). Two prey taxa occurred in 5.0–10.0% of the scats: Pacific mackerel *Scomber japonicus* (9.5%) and octopus, *Octopus* spp. (5.1%). We identified 17 species and two genera of fish, and two species and one genus of cephalopod not reported previously as prey of California sea lions (Table 2).

Nearly half of the scats (46.1%) contained only one prey taxa (Fig. 2). Northern anchovy constituted 56.2% of 603 scat samples with single prey taxa (Fig. 3).

### Variability in diet through time

We found differences in distributions of occurrence (occurrence and composition indices) and numbers of individuals (number index) for nine prey taxa examined for temporal variability during the pre-El Niño, El Niño, and post-El Niño periods (Fig. 4). The distributions of occurrence were significantly different for Pacific whiting, northern anchovy, jack mackerel, Pacific mackerel, market squid, octopus and pelagic red crab ($P<0.01$). Northern anchovy occurred frequently and in the highest numbers of any prey taxa in all three periods. During the pre-El Niño period, jack mackerel occurred in the scat samples more often than the other prey; and jack mackerel and market squid were found in greater indi-

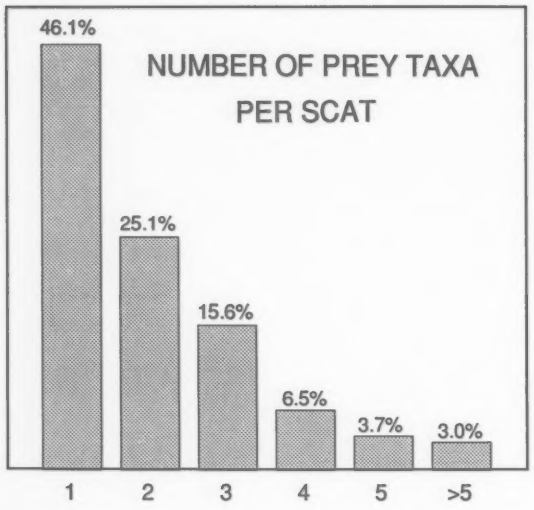



**Figure 2**

Occurrence of single and multiple prey taxa in 1309 California sea lion scats collected at San Clemente Island, California.

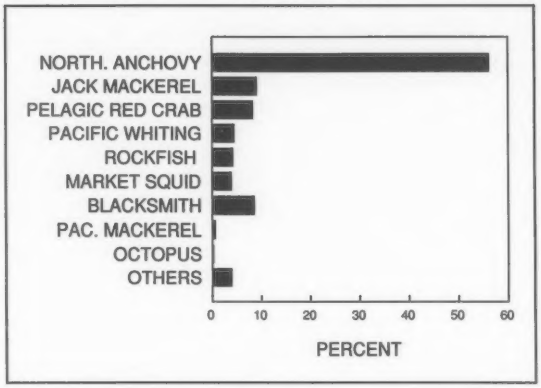
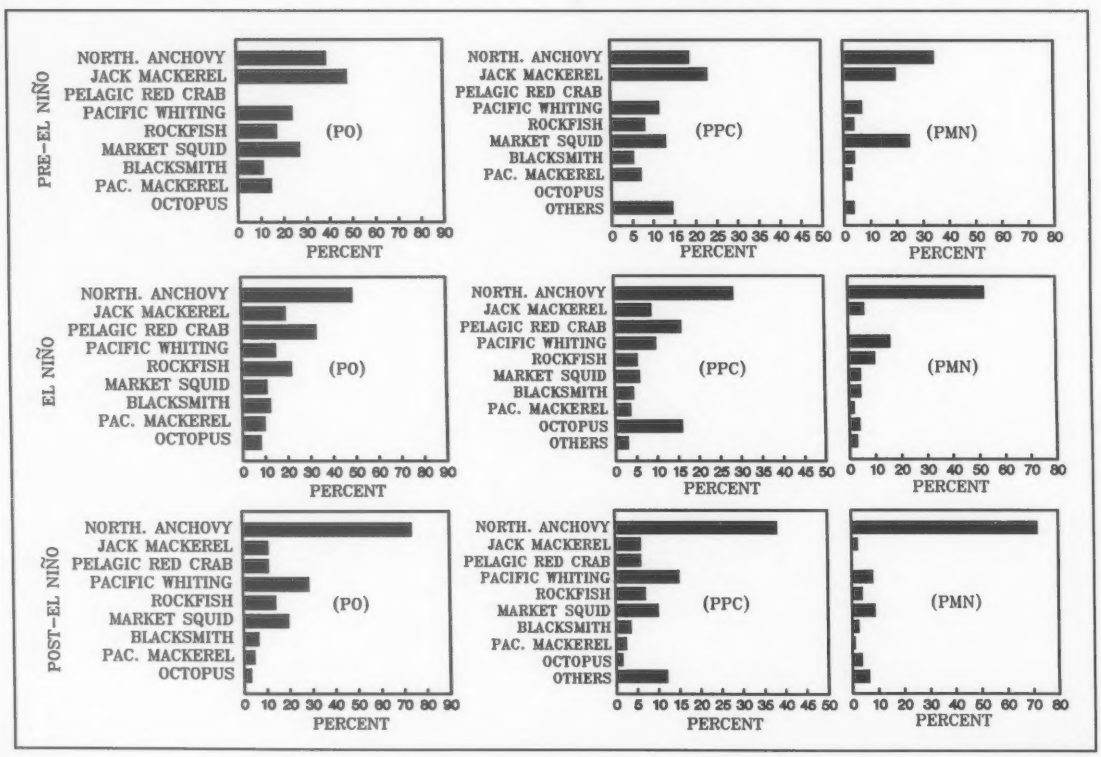



**Figure 3**

Percent prey found in 603 California sea lion scats with single prey taxon.

**Figure 4**

Occurrence (PO), composition (PPC), and number (PMN) indices of 9 prey taxa found in 1309 California sea lion scats collected at San Clemente Island, California, 1981–86, which are divided into pre-El Niño (September 1981–August 1982), El Niño (November 1982–September 1984), and post-El Niño (November 1984–September 1986) periods. The number index (PMN) could not be determined from fragments of pelagic red crab.



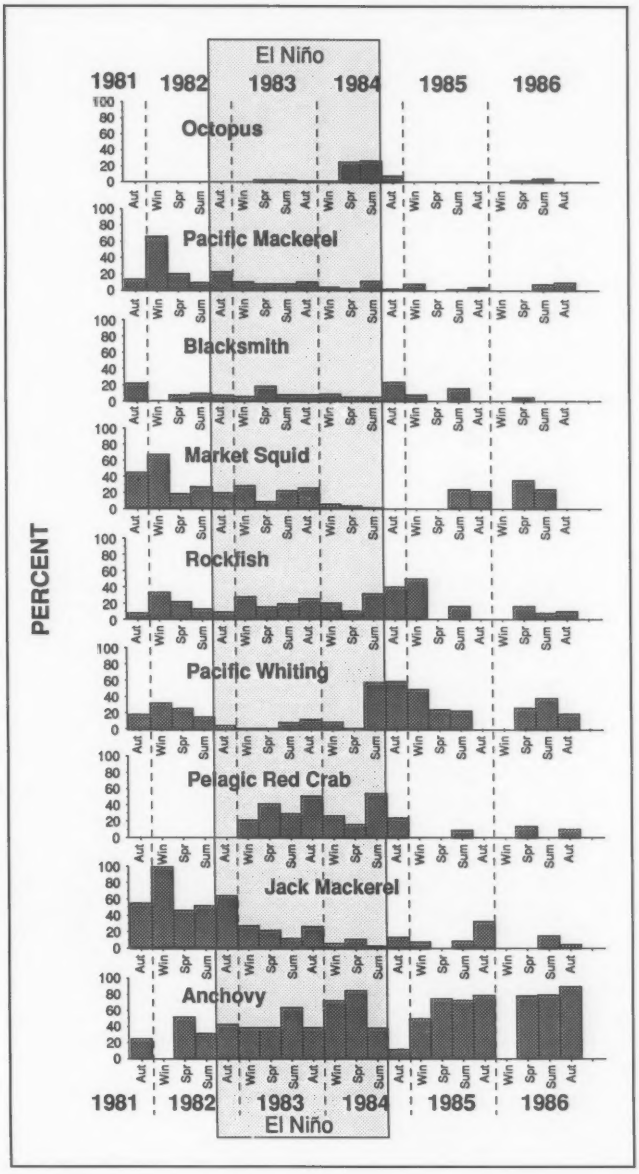



**Figure 5**
Seasonal percent occurrence (PO) of 9 prey taxa found in 1304 California sea lion scats, 1981–86. No samples were collected in winter 1986.

vidual numbers than other prey taxa, except northern anchovy. During the El Niño period, pelagic red crab were the second most frequently occurring prey in scat samples. During the post-El Niño period, the diet was dominated by northern anchovy.

We found yearly and seasonal variability in the relative proportions represented by the three indices for 9 prey taxa examined (Figs. 5–7). Northern anchovy was consistently found in scats throughout the study at varying occurrence, composition, and number index levels. However, during summer and autumn 1984 we noted a drop in the three indices compared with 1982, 1983, 1985, and 1986; and it did not occur as often in 1982 as in 1983, 1985, and 1986. Jack mackerel was the most frequent prey during 1981–82, but after that period it was found infrequently, represented a very small proportion of the diet, and few individuals were found in the scats. An increase in the occurrence of

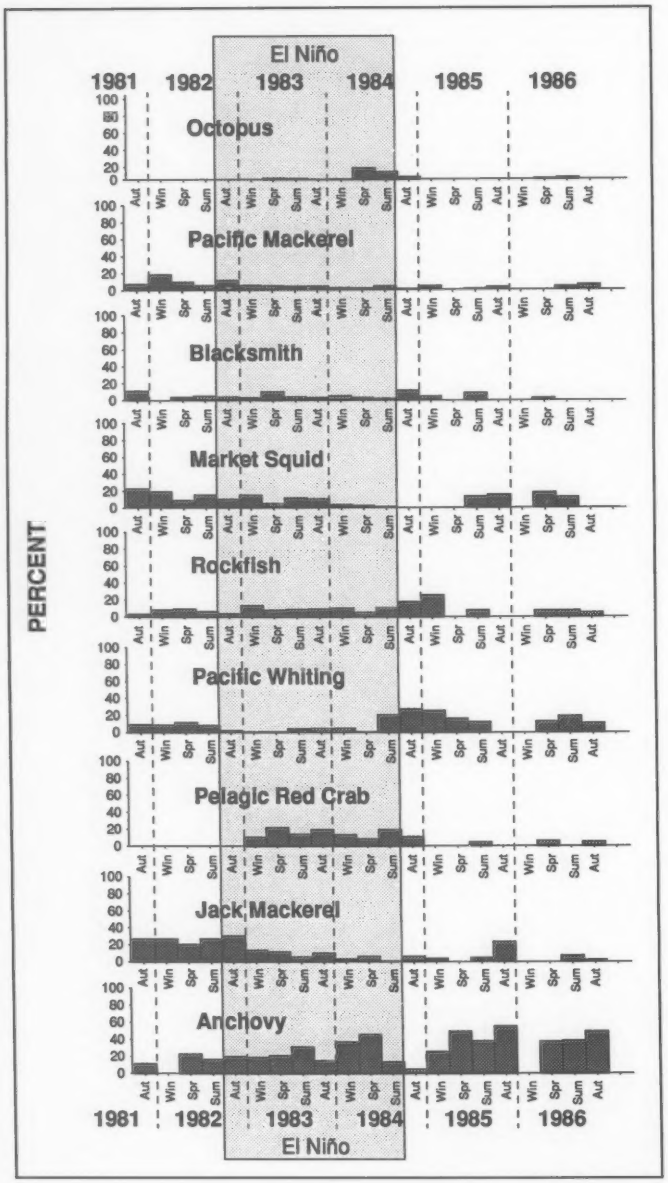



**Figure 6**
Seasonal percent prey composition (PPC) of 9 prey taxa found in 1304 California sea lion scats, 1981–86. No samples were collected in winter 1986.

Pacific whiting was found during summer–autumn 1984 and winter 1985 when many individuals were found in scats. Rockfish was consistently found in scats throughout the study, but more individuals were represented during summer–autumn 1984 and winter 1985 than other times. Market squid was found in extremely low occurrence, composition, and number index levels ($\leq$5.6%) or was absent from scat samples from winter 1984 through spring 1985. Pelagic red crab occurred primarily during the 1983–84 California El Niño period. Pacific mackerel occurred in the scat samples more often in 1982 than during the following years, but was represented by few individuals from 1981 to 1986. Blacksmith occurred in scat samples throughout the 1981–84 period, but during the 1985–86 period it occurred inconsistently in the diet. Octopus appeared in the samples from spring 1983 to autumn 1984, and spring–summer 1986.

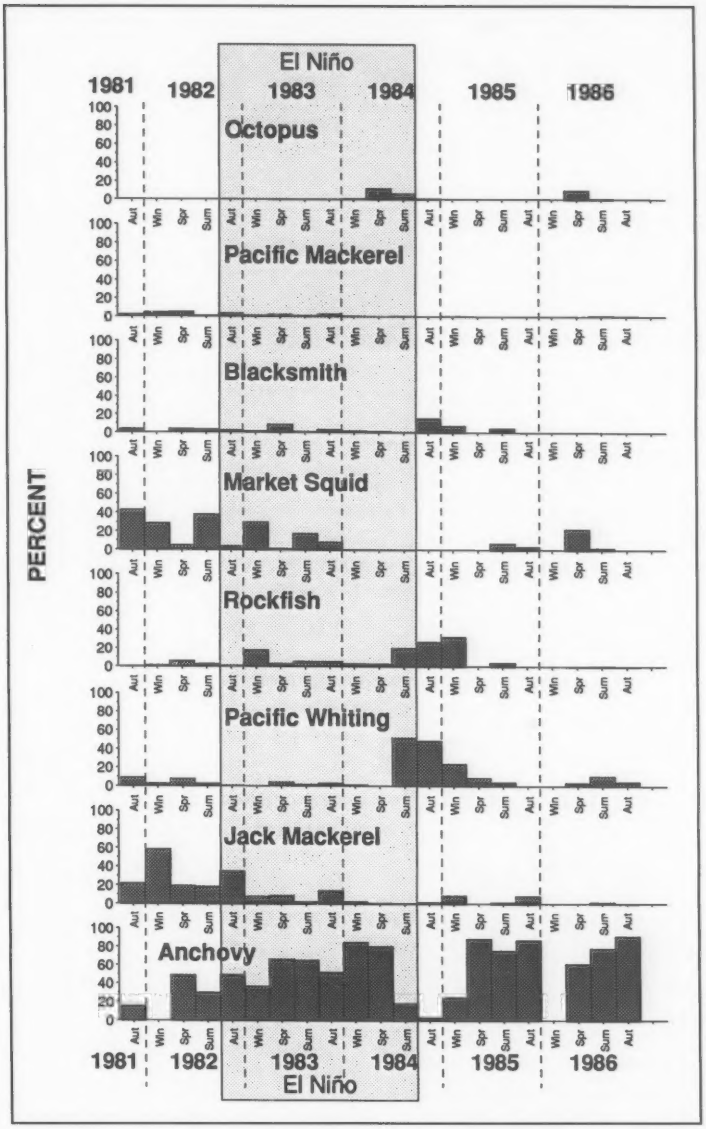



**Figure 7**
Seasonal percent minimum number (PMN) of 8 prey taxa found in 1304 California sea lion scats, 1981–86. No samples were collected in winter 1986. PMN could not be determined from fragments of pelagic red crab.

Analyses of the three-season-five-year and four-season-four-year data sets indicated significant differences ($P \leq 0.05$) in the occurrence of some, but not all, of the nine prey tested. Variances of occurrence were significantly different for all nine prey (Levene's test, $P \leq 0.05$). The three-season-five-year data set showed 21 significant differences in year, season, or season-year interactions, and the four-season-four-year data set showed 14 significant differences in year, season, or season-year interactions. Because the three-season-five-year data set included more of the post-El Niño period, results from that data set were used to interpret seasonal and yearly changes in prey items. Northern anchovy, jack mackerel, Pacific whiting, and octopus showed significant seasonal, yearly, and season-year interaction differences ($P<0.01$). Pelagic red crab, rockfish, market squid, and blacksmith showed only significant yearly and season-year interactions differences ($P<0.01$). Pacific mackerel had a significant difference only among years ($P<0.01$).

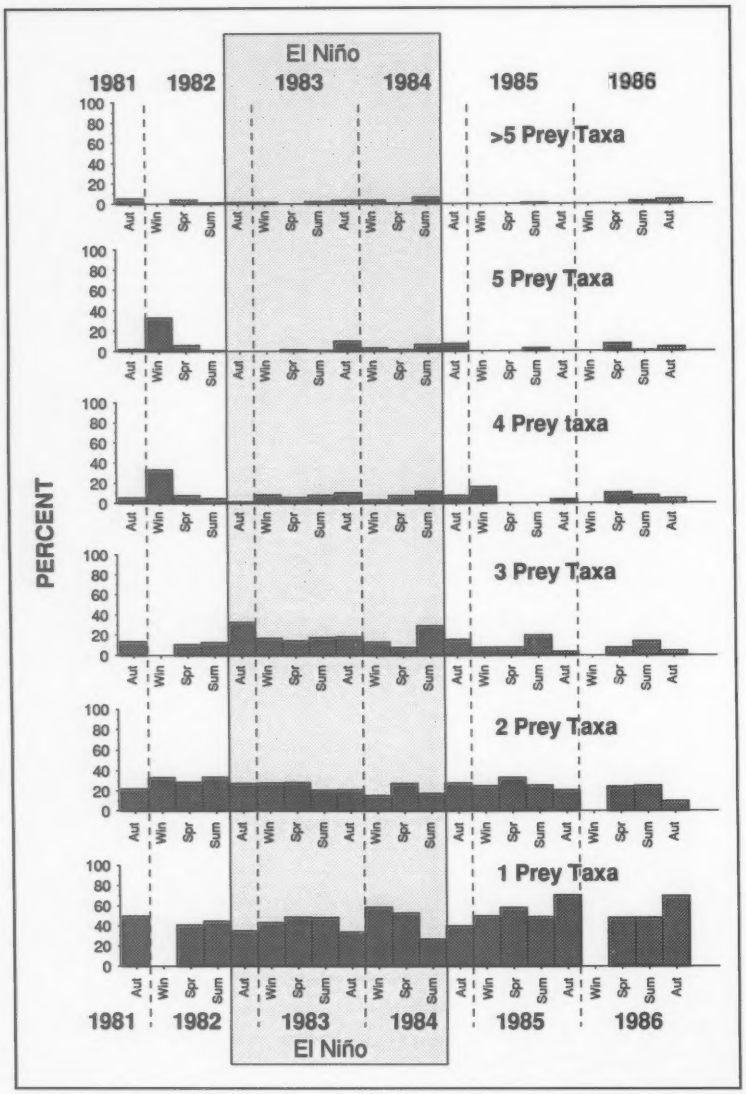



**Figure 8**
Seasonal occurrence of single and multiple prey taxa found in 1304 California sea lion scats, 1981–86. No samples were collected in winter 1986.

The relative frequencies of different prey taxa per scat varied among seasonal sampling periods during the study period (Fig. 8). Relative frequencies of prey taxa per scat for years 1982–85 were the same for all seasons in 1983 ($\chi^2 = 22.067$, df = 15, $P = 0.1061$) and 1985 ($\chi^2 = 18.219$, df = 15, $P = 0.2513$), but greater numbers of prey taxa were found in scats in 1982 ($\chi^2 = 35.892$, df = 15, $P = 0.0018$) and 1984 ($\chi^2 = 44.046$, df = 15, $P = 0.0001$).

## Discussion

California sea lions using SCI consumed a variety of prey, consisting primarily of fish and cephalopods as indicated by the presence of fish remains in 98.5% of the scats and cephalopod remains in 35.5% of the scats. They fed on schooling fishes (e.g., northern anchovy, jack mackerel, Pacific mackerel, Pacific whiting, blacksmith, and rockfish), schooling cephalopods (e.g., market squid; Hurley 1978), and pelagic crustaceans that drift in large swarms (e.g., pelagic red crab; Boyd 1967). Our temporal analysis of nine prey taxa in-

dicated seasonal and yearly variability in the diet of SCI sea lions. Northern anchovy apparently was the major food source because it was represented by high index values and consistently occurred in the sea lions' diet during the 5-year period. Pelagic red crab, jack mackerel, Pacific whiting, rockfish, market squid, blacksmith, and Pacific mackerel appear to supplement the diet of California sea lions.

A major uncertainty with using scat analysis to study pinniped food habits is how these results reflect what was initially consumed by the animals. Studies on captive pinnipeds indicate that recovery rates are (1) lower than ingestion rates for all prey; (2) lower for prey species with small otoliths than prey with large otoliths; and (3) lower for young (i.e., small) prey than for older (i.e., large) prey of the same species (Hawes 1983, da Silva and Neilson 1985, Murie and Lavigne 1986, Dellinger and Trillmich 1988, Harvey 1989). Proportions of different prey species in scats were found to correspond to proportions of prey fed (Dellinger and Trillmich 1988). Pitcher (1980) found no difference between occurrence of fish in stomachs and feces of harbor seals *Phoca vitulina*, but cephalopods were under-represented in their feces.

The prey that occurred in 10% or more of scat samples ranged from small-sized (i.e., northern anchovy, market squid, and pelagic red crab) to prey that, when mature, could be potentially large-sized (i.e., Pacific whiting, jack mackerel, rockfish, and Pacific mackerel). Northern anchovy, being small-sized with small otoliths, would probably represent a higher proportion of the diet than indicated in scat samples. Market squid would also represent a higher proportion of the diet because beaks are often regurgitated and would be underrepresented in scats.

Results from SCI indicated differences in both prey composition and temporal variability from those described by Bailey and Ainley (1982) for sea lions at the Farallon Islands off central California. We found that several prey were consistently consumed (e.g., northern anchovy, jack mackerel, Pacific whiting, rockfish, market squid, blacksmith, and Pacific mackerel), whereas they reported only two prey (Pacific whiting and rockfish) that were regularly eaten. They found Pacific whiting to occur in the sea lions' diet during spring and summer, and juvenile rockfish during the fall and winter. At SCI we found that the presence of various types of prey in the diet of sea lions fluctuated year-to-year and sometimes seasonally within the same year. These differences between two island areas may be due to differences in the sampling periods (1981–86 for our study; 1974–78 for the Farallon Island study), to differences in prey availability in each area, or to differences in the sexual composition of animals inhabiting each area.

We would expect similar diets for sea lions using islands within close proximity of each other. Data from a study of food habits on San Miguel Island (SMI) during spring and summer in 1978–79 by Antonelis et al. (1984) were compared with our results. Four types of prey taxa (Pacific whiting, rockfish, northern anchovy, and market squid) were consistently found in scats of SCI and SMI sea lions. Jack mackerel, consistently found at SCI, was a minor prey item at SMI. The presence of pelagic red crab at SCI was due to the California El Niño, which did not occur during the SMI study. Blacksmith were not found in the diet of sea lions at San Miguel Island, but occurred frequently in the SCI study. Because the distribution and availability of these prey differ over time, we are unable to test our expected similarities in prey consumption until concurrent studies are conducted.

Availability and abundance of sea lion prey have been demonstrated by Bailey and Ainley (1982) and Antonelis et al. (1984) to influence diet of California sea lions. Evidence that abundance, if not availability, of prey influences consumption is also found from our study at SCI when we compare anchovy occurrence in scats with anchovy biomass estimates for each year (Bindman 1986, Methot and Lo 1987). The decline in the occurrence of anchovy in the scats during 1982 and 1984 coincided with lower estimates of anchovy biomass of 415,000 mt for 1982 and 309,000 mt for 1984 (Bindman 1986). Increased occurrence of anchovy in scats during 1983, 1985, and 1986 coincided with greater estimates of anchovy biomass: 623,000 and 522,000 mt (Bindman 1986), and 764,000 mt (Methot and Lo 1987), respectively. Decline in anchovy biomass may have caused SCI sea lions to consume other species in 1982 and 1984, resulting in increased occurrence in the latter.

There was more variability in occurrence of different prey taxa per scat in 1982 and 1984 when the estimated population biomass of anchovy was low, and less variability in 1983 and 1985 when there was a greater biomass. The diet of SCI sea lions, therefore, may be strongly affected by the abundance of northern anchovy. As anchovy becomes scarce, we expect SCI sea lions to consume other types of prey and exhibit greater variability in the number of different prey consumed.

We expected the non-El Niño periods to have similar occurrences of prey taxa consumed, which would differ from the El Niño distribution. In fact, all three periods exhibited significantly different distributions of prey taxa and in their occurrence.

The pattern in the commercial harvest of market squid (which is not affected by regulations and quotas) observed in California before, during, and after El Niño (Worcester 1987) closely resembled the pattern observed in the occurrence of this prey in the diet of SCI

sea lions. During the El Niño in 1983 and 1984 the commercial catch of market squid was 2010 and 622 short tons, respectively; prior to the El Niño it was 25,915 and 17,951 short tons for 1981 and 1982, respectively; and, after the El Niño it was 11,326 and 23,124 short tons for 1985 and 1986, respectively. The presence of market squid in the diet of sea lions during 1983 indicates the availability of this prey to sea lions, despite low availability to commercial catches. However, in 1984 when the commercial harvest was at its lowest, market squid was not detected in the sea lions' diet. Both the sea lions' consumption of market squid and the commercial catch were apparently affected by availability.

The effect of El Niño on the diet of SCI sea lions is also demonstrated by the presence of remains from pelagic red crabs in scat samples. Pelagic red crabs are normally found over the continental shelf of southern Baja California, and are sometimes transported into the SCB and further northward by the Davidson and California Countercurrents in January and February (Boyd 1967). These currents intensified as a result of the 1982–83 El Niño/Southern Oscillation, affected water temperatures in the SCB from late 1982 to October–November 1984, and carried pelagic red crabs from southern Baja California to the SCB where they were eaten by California sea lions.

The food consumed by the U.S. population of California sea lions could have an impact on the ecosystem and be in direct competition with commercial and sport fisheries. Six of the common prey of California sea lions identified at SCI (jack mackerel, northern anchovy, market squid, Pacific mackerel, Pacific whiting, and rockfish) are of value to commercial or sport fisheries. DeMaster (1983) estimated that California sea lions in U.S. waters (estimated population size 69,700) consumed roughly 115,000–295,000 mt of biomass per year. The present consumption would be greater than in 1983 because of the estimated 5% annual increase in the U.S. population (DeMaster et al. 1982). The growth in the sea lion population, and its estimated consumption, raises questions. Will there be greater competition between sea lions and fishermen for fish and squid as a result of increased numbers of sea lions? What will be the effect of population growth of sea lions on other elements of the SCB ecosystem?

Observed temporal differences in diet of sea lions from SCI during the California El Niño of 1982–84 clearly indicate the need for long-term studies of food habits of this predator throughout its range. Short-term studies may reflect oceanographic conditions of relatively short duration, such as El Niño, that strongly influence food supply and sea lion diet.

## Acknowledgments

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# Reproduction, Age, and Growth of the Whitemouth Croaker *Micropogonias furnieri* (Desmarest 1823) in Trinidad Waters

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**Abstract.**– Reproduction, age, growth, and mortality of the whitemouth croaker *Micropogonias furnieri* in Trinidad, West Indies, were studied. Maturity was attained at 2 years of age for both sexes. Spawning occurred year-round with a peak from February to August. The condition factor varied with the reproductive cycle. The sex ratio was 1:1.3 male:female. Fecundity ranged from $17\times10^3$ to $37\times10^5$ eggs for fish measuring 27.6–57.2 cm total length. Relationships between fecundity ($F$) and total length (TL) in centimeters, and body weight (W) and ovary weight (Wg) in grams, respectively, were: $F = 2\times10^{-4}TL^{5.56}$; $F = 0.81\ W^{1.88}$, and $F = 22525\,Wg - 81355$. The length-weight relationship was $W = 0.037\,TL^{2.64}$. Age was determined using otoliths and the analysis of length-frequency distributions. The von Bertalanffy growth equations were $L_t = 65.3\ \{1 - \exp[-0.16(t + 1.6)]\}$ for males and $L_t = 82.9\{1 - \exp[-0.13(t + 1.3)]\}$ for females. Total mortality rate was 1.2/year, natural mortality rate 0.4/year, and fishing mortality 0.8/year. Yield-per-recruit analysis showed the whitemouth croaker to be fully exploited in Trinidad.

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The whitemouth croaker *Micropogonias furnieri* (Desmarest 1823) is found in most of the Antilles, and along the southern Caribbean coast and Atlantic coast of South America from Costa Rica to Argentina (Fischer 1978). Important fishing grounds extend from Venezuela to Uruguay. This species is one of the most economically important demersal fish in Trinidad, where it is caught mainly by trawling and bottom longlines. Juvenile croakers also constitute a significant portion of the shrimp bycatch, most of which is discarded at sea.

Relevant studies have been conducted in Brazil and include general biology (Vazzoler 1962); age and growth (Rodrigues 1968); reproduction, population diversification, and growth (Vazzoler 1970, 1971); feeding habits (Tanji 1974); growth and sexual maturation of juveniles (Castello 1982); and reproductive biology (Isaac-Nahum and Vazzoler 1983).

Presented in this paper are some aspects of the biology, including reproduction, growth, mortality, and yield-per-recruit (Y/R) analysis, of the croaker in Trinidad waters.

## Materials and methods

### Study area

The island of Trinidad lies between lat. 10°2′N and 10°50′N and long. 60°54′ and 61°56′W on the South American Continental Shelf. Wide expanses of flat, muddy, relatively shallow substrate are found in the coastal areas where trawling for demersal fish and penaeid shrimps is carried out. The climate is tropical with a dry season from January to June and a wet season from July to December. Sampling was done in the northwestern waters of Trinidad in depths of 30–60 m.

### Methods

Between October 1977 and September 1982, 2314 croakers were obtained by trawling. The vessels were of steel hull, 25–29 m in length, and carrying two side trawls. The opening of the trawl nets ranged from 13.7 to 18 m at the head end while the cod end mesh size was 2.5 cm. The catch was sorted into species and placed in separate baskets, each with a capacity of about 32 kg. Depending on the size of the catch, 2–3 baskets of croaker were taken at random for analysis. Total length (TL) in centimeters, body weight (W) and gonad weight (Wg) in grams, and sex and gonad maturity stage were recorded.

Four maturity stages were recognized macroscopically (following Vazzoler 1971): immature, maturing, mature (ripe), and spent. Mature ovaries were weighed to the nearest gram

and preserved in Gilson's fluid (Simpson 1951), and fecundity determined using a volumetric method (Bagenal and Braum 1971). Condition factor (CF) was determined from the formula $CF = 100\,W/TL^3$ (Hile 1936).

Age was determined using otoliths (sagittae) from a total of 252 fish. Longitudinal sections of otoliths were prepared following the technique described by Holden and Raitt (1974). Sections were wet with water and viewed against a black background using reflected light. Distinct alternating broad opaque and narrow translucent rings were present and the latter were assumed to be annuli. Rings were determined to be annual by using the marginal increment technique (e.g., Moe 1969, Turner et al. 1983). Otoliths were reread by the same worker one month after the initial reading and a 90% agreement was found, while a 92% agreement was found with another worker's readings. Marginal increment and otolith radius were measured using an ocular micrometer (1 micrometer unit = 0.05 mm).

Attempts were also made to determine age by analyzing the length-frequency distribution using cumulative probability paper. Total length was plotted against percentage cumulative frequency, resulting in a Cassie curve (Cassie 1954). Age groups were separated using points of inflexion which were chosen by eye. Only fish caught during March–May 1978 were used in this analysis.

The von Bertalanffy (1938) model was used to describe growth:

$$L_t = L_\infty \{1 - \exp[-K(t - t_0)]\}$$

where $L_t$ is length at time $t$, $K$ is the growth coefficient, $L_\infty$ is the asymptotic length, and $t_0$ is the hypothetical age at zero length. These parameters were estimated utilizing the Length Based Fish Stock Assessment (LFSA) Package of BASIC computer programs (Sparre 1987).

Total annual mortality rate ($Z$) was estimated from a length-converted catch curve (Pauly 1984). Natural mortality rate ($M$) was determined from the empirical relationship derived by Pauly (1980):

$$\log M = 0.0066 - 0.279 \log L_\infty + 0.6543 \log K + 0.4634\, T,$$

where $T$ is the mean water temperature which was 26.2°C in this area. Fishing mortality ($F$) was calculated as the difference between $Z$ and $M$ (Ricker 1975).

Yield per recruit (Y/R) in grams was determined from the model of Beverton and Holt (1957). Analyses were carried out using the LFSA package. The input parameters were $W_\infty$ (determined from the formula $W = a\,L_\infty^b$), $K$, $t_0$, $M$, $t_c$ (age at first capture of 2 years), which was determined by mesh selectivity experiments (Sylvester 1986), and $t_r$ (age at recruitment). Examination of length-frequency distributions of catches indicated that croakers were fully recruited at a total length of 25 cm, or 1 year of age. The average values of $K$ and $t_0$ for both sexes were used. Y/R analysis was done for a range of $M$ values to determine their effects on conclusions drawn.

**Table 1**
Percentage of mature male and female croaker by size group in Trinidad waters.

| Total length (cm) | Percentage mature | |
|---|---|---|
| | Male | Female |
| 22–24 | 1 | 4 |
| 24–26 | 6 | 20 |
| 26–28 | 44 | 16 |
| 28–30 | 61 | 17 |
| 30–32 | 67 | 49 |
| 32–34 | 74 | 70 |
| 34–36 | 97 | 85 |
| 36–38 | 97 | 89 |
| 38–40 | 97 | 96 |
| 40–42 | 100 | 100 |
| 42–44 | 100 | 100 |
| 44–46 | 100 | 100 |
| 46–48 | 100 | 100 |
| 48–50 | 100 | 100 |
| 50–52 | 100 | 100 |
| 52–54 | 100 | 100 |
| 54–56 | — | 100 |
| 56–58 | — | 100 |

## Results

### Size at maturity

The percentage of mature males and females in each 3-cm size group is shown in Table 1. The size at which 50% of the fish examined were mature was about 28 cm for males and 32 cm for females.

### Spawning pattern

Examination of the monthly frequency of croakers in each developmental stage showed the presence of all stages throughout the year (Table 2). A higher percentage of ripe fish was found from February to August, indicating an intensification of spawning during this time.

### Sex ratio

The overall sex ratio of 852 croakers was 1:1.3, male: female. This was significantly different from 1:1 ($P$

**Table 2**
Monthly percentages of croaker by developmental stage in Trinidad waters.

| Maturity stage | J | F | M | A | M | J | J | A | S | O | N | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Immature | 33 | 32 | 23 | 2 | 25 | 48 | 27 | 19 | — | 15 | 23 | 37 |
| Maturing | 11 | 34 | 48 | 27 | 40 | 42 | 40 | 32 | — | 52 | 58 | 59 |
| Mature | 17 | 32 | 20 | 27 | 24 | 10 | 18 | 27 | — | 10 | 4 | 3 |
| Spent | 39 | 2 | 9 | 44 | 11 | 0 | 15 | 22 | — | 23 | 15 | 1 |
| *N* | 18 | 47 | 141 | 59 | 63 | 42 | 337 | 81 | — | 134 | 116 | 80 |

<0.001). Monthly sex ratios showed a higher proportion of females from March to October and of males from November to February.

## Fecundity

Fecundity estimates for 24 fish measuring 27.6–57.2 cm ranged from $17\times10^3$ to $37\times10^5$ eggs. Mean number of eggs per gram ovary-free body weight was 449 with a standard deviation of 169. Relationships between fecundity and total length, body weight, and ovary weight were described by the following respective regressions:

$$F = 2 \times 10^{-4}TL^{5.56} \quad (r^2 = 0.90)$$

$$F = 0.81W^{1.88} \quad (r^2 = 0.89)$$

$$F = 22525Wg - 81355 \quad (r^2 = 0.99)$$

## Length-weight relationship

The length-weight relationship for males was $W = 0.035TL^{2.66}$ and for females $W = 0.030TL^{2.69}$. Analysis of covariance showed no significant difference between the two sexes ($P>0.05$), therefore the data were pooled and one relationship established: $W = 0.03TL^{2.64}$. Asymptotic weight ($W_\infty$) was 3641.6 g.

## Condition factor

Monthly variation in condition factor for males and females is shown in Figures 1 and 2, respectively. The condition factor was lowest in August for both sexes while it was highest in April for males and in May for females.

## Age and growth

Mean marginal increments were lowest from May to August, indicating that annulus formation occurred during this period (Fig. 3). Fish length was directly proportional to, and highly correlated with, otolith radius (R): $TL = 12.0 + 32.7R$, ($r^2 = 0.94$). Otolith reading showed the presence of six age groups for males and seven for females, while analysis of length-frequency

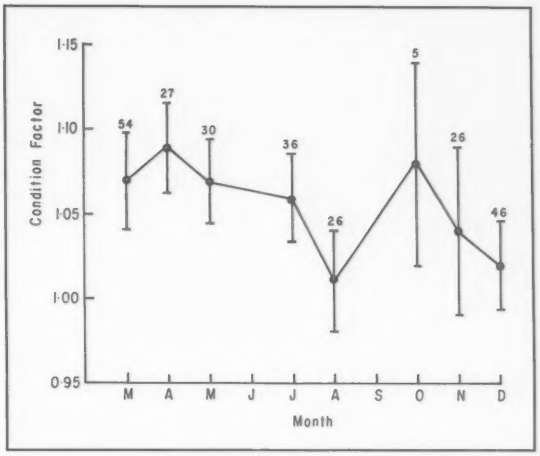


**Figure 1**
Mean monthly condition factor (±95% CL) of male croaker in Trinidad waters. Number of fish is given for each month.

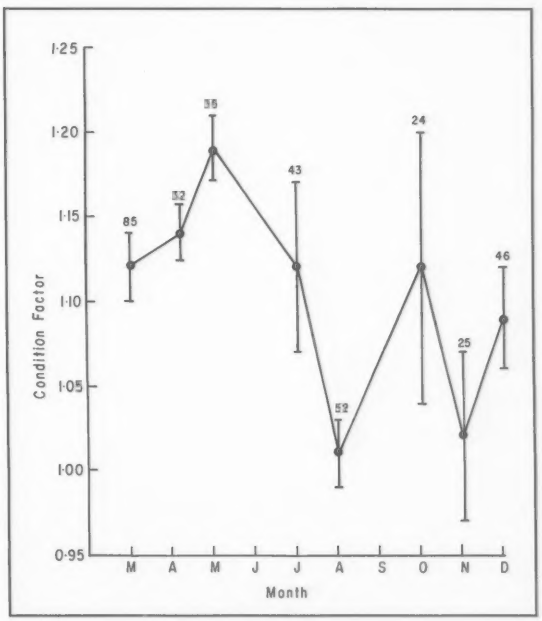


**Figure 2**
Mean monthly condition factor (±95% CL) of female croaker in Trinidad waters. Number of fish is given for each month.

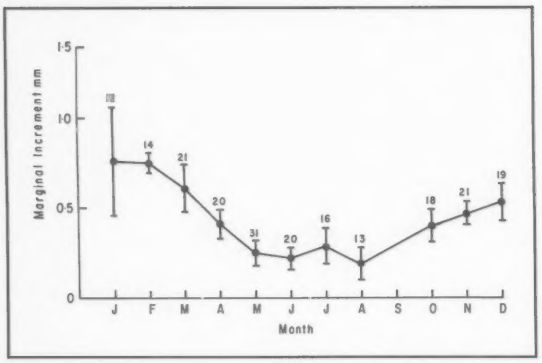


**Figure 3**
Mean monthly marginal increment (±95% CL) of otoliths of the croaker in Trinidad waters. Number of fish is given for each month.

distribution of combined sexes showed six age groups (Fig. 4). There was close correspondence in lengths at respective ages found by the two methods (Table 3). Based on the above, use of otoliths for age determination of the croaker is considered to be valid. A preliminary plot of the observed length at age revealed that growth of the croaker could be adequately described by the von Bertalanffy equation. Growth parameters showed that females achieved a greater asymptotic length, but grew at a slower rate than males. In Table 4 these parameters are compared with those found for different populations of croaker in Brazil.

### Mortality

Total mortality rate ($Z$) which was the slope of the descending part of the length-converted catch curve in Figure 5 was 1.2/year ($r^2 = 0.96$, $P<0.05$). The 95% confidence limits for $Z$ were 0.91 and 1.49. Natural mortality rate ($M$) was 0.4/year, and fishing mortality rate ($F$) was 0.8/year.

### Yield per recruit

At the present level of $F$ and $t_c$, Y/R is already at the maximum of 175 g (Fig. 6). Increasing $F$ results in a decrease in Y/R. Increasing $t_c$ to 3 years results in a Y/R of 181 g at the same level of $F$. At values of $M$ of 0.1, 0.2, and 0.3 the croaker is overexploited at the corresponding levels of $F$ (Fig. 7), while at $M$ of 0.4 and 0.5 it is fully exploited. At low $M$ values the yield curves are domed with peaks at low $F$ values, while at higher $M$ values they are relatively flat.

## Discussion

Several similarities exist in the reproductive biology of the whitemouth croaker throughout its geographical range. Early maturity and year-round spawning have

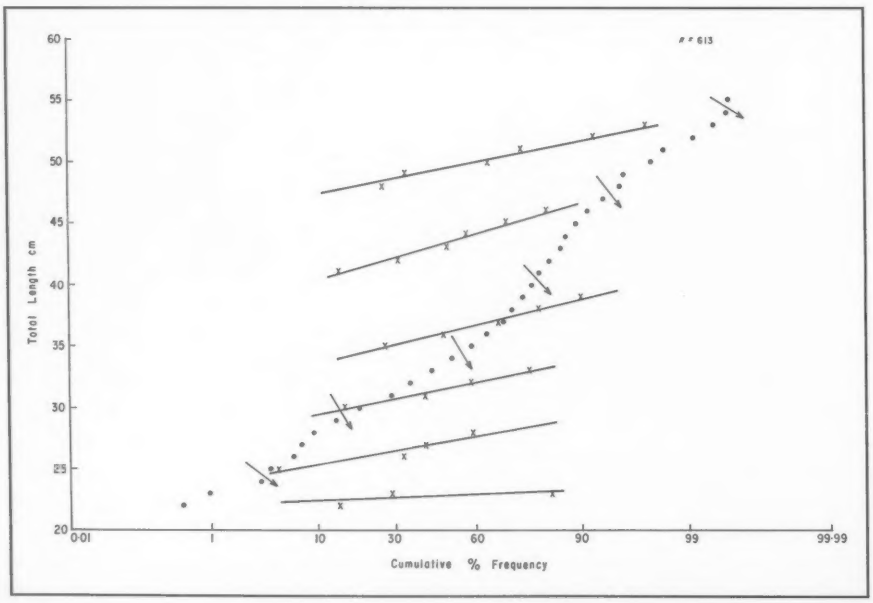


**Figure 4**
Cumulative percentage length-frequency curve (dotted line) and separation into six age groups (straight lines) for the croaker in Trinidad waters. Arrows indicate inflexion points chosen by eye.

**Table 3**
Mean length at age determined from otolith sections and length-frequency distribution of the croaker in Trinidad waters.

| Age group | Otoliths (TL ± SD) Male | *N* | Female | *N* | Length-frequency distribution (±SD) |
|---|---|---|---|---|---|
| I | 22.0 ± 1.92 | 26 | 21.6 ± 2.09 | 23 | 22.3 ± 0.35 |
| II | 28.3 ± 1.85 | 21 | 29.4 ± 2.71 | 34 | 27.3 ± 1.65 |
| III | 33.6 ± 1.49 | 14 | 34.2 ± 1.89 | 18 | 31.6 ± 1.65 |
| IV | 38.5 ± 2.36 | 29 | 40.5 ± 1.98 | 30 | 36.2 ± 2.05 |
| V | 42.5 ± 1.83 | 10 | 47.5 ± 2.94 | 12 | 43.5 ± 2.45 |
| VI | 45.6 ± 2.79 | 10 | 51.6 ± 2.90 | 14 | 49.5 ± 1.70 |
| VII | — — | — | 53.5 ± 3.25 | 11 | — — |

**Table 4**
von Bertalanffy growth parameters of the croaker in Trinidad and Brazil waters.

| Area | Sex | $L_\infty$ | $K$ | $t_0$ | Structure | Author |
|---|---|---|---|---|---|---|
| Brazil (33–29°S) | F | 69.33 | 0.149 | −2.79 | scales | Vazzoler 1971 |
| | M | 89.57 | 0.076 | −4.64 | | |
| Brazil (29–23°S) | F | 60.10 | 0.219 | −2.08 | scales | Vazzoler 1971 |
| | M | 82.90 | 0.106 | −2.97 | | |
| Brazil (4°S) | F | 67.60 | 0.18 | −0.42 | scales | Rodrigues 1968 |
| | M | 68.60 | 0.18 | −0.52 | | |
| Trinidad | F | 82.90 | 0.13 | −0.13 | otoliths | This study |
| | M | 65.30 | 0.16 | −0.16 | | |

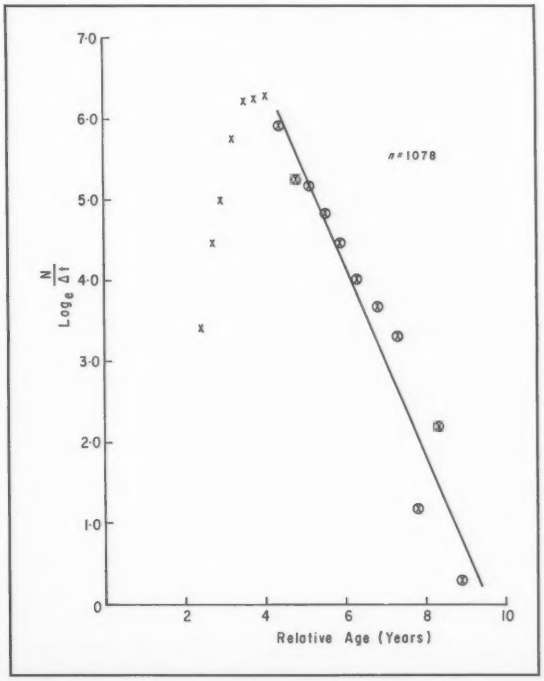


**Figure 5**
Length-converted catch curve of the croaker in Trinidad waters. (⊗) points used to find *Z*; (x) ascending part of curve, not used in analysis.

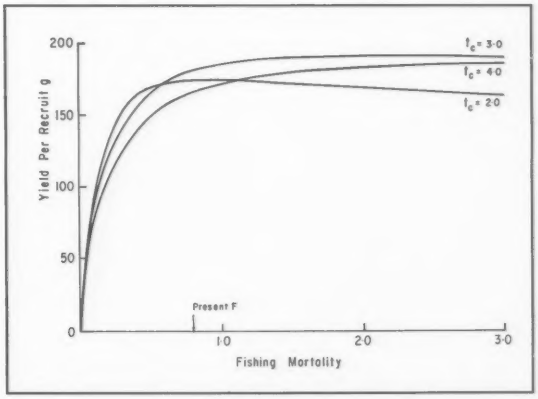


**Figure 6**
Yield per recruit (g) of croaker in Trinidad waters against fishing mortality for age at first capture of 2, 3, and 4 years.

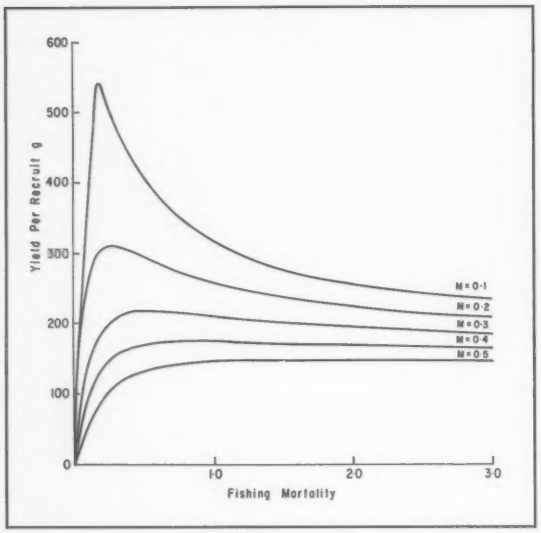


**Figure 7**
Yield per recruit (g) of croaker in Trinidad waters against fishing mortality for natural mortality rates of 0.1, 0.2, 0.3, 0.4, and 0.5 per year.

also been recorded in Brazil (Vazzoler 1962, 1971; Castello 1982; Isaac-Nahum and Vazzoler 1983), and in Guyana (Lowe-McConnell 1966).

Other workers have been successful in determining the age of tropical and subtropical sciaenids using otoliths (e.g., Bayagbona 1969, Villyamar 1972, Pannella 1974, Barger 1985). Annulus formation coincides with both the period of peak spawning and the wet season when salinity decreases due to river run-off. A similar pattern occurs in other species of tropical sciaenids (e.g., Rao 1966, Le Guen 1971). The annulus in immature croaker is probably formed in the wet season of the year following their year of birth. Use of the Cassie method had two disadvantags: the subjectivity in choosing the inflexion points and the crowding of older age groups into the upper part of the cumulative frequency curve. However, the close agreement of results obtained by both methods validates the use of otoliths for age determination of the croaker.

The higher value of $K$ for males than for females suggests a higher mortality rate for the former (Beverton and Holt 1959). This could also account for the presence of only six age groups for males and the predominance of females in the population.

The variation in growth between Trinidad and Brazil indicates that the croaker does not present a uniform population in this region. According to Vazzoler (1971) geographical differences in growth characteristics of this species are due to genotypical and ecological factors such as salinity and temperature.

Estimation of mortality rates from length-converted catch curves is subject to several assumptions, the most important of which is that of constant recruitment (Ricker 1975). Examination of length-frequency distributions indicated that the modal length in the catch was similar for all years of sampling (33.0–34.9 cm), and no particularly strong or weak year class was apparent. Another assumption is that of constant fishing effort, which did not change appreciably during the period of sampling, as indicated by the number of active vessels. Since only fully recruited age groups were used in this analysis, $Z$ was assumed to be constant over these ages. Trawling was considered to be a random method of sampling for older, fully recruited age groups, and the sample was assumed to be representative of that part of the population which was used to compute $Z$. Violation of these assumptions often results in non-linear right limbs of catch curves (Ricker 1975). However, the linear right limb of the catch curve in this study and the significant regression suggest that the estimate of $Z$ is acceptable.

All of the conditions, except that of isometric growth, accompanying the Beverton and Holt model are assumed to exist for the croaker. The assumption of isometric growth, when growth is in fact allometric, leads to incorrect estimates of yield (Paulik and Gales 1964). However, the absolute levels of these estimates are not of as much interest as the differences in yield that result from varying $t_c$ and/or $F$. The relative error in such differences, when using an incorrect $b$, tends to be much less than that in the absolute levels (Ricker 1975).

Locally, fishing is the major cause of mortality of the croaker. At the present $t_c$ and the level of $F$ the maximum sustainable Y/R is already being obtained, and any increase in $F$ would result in overexploitation. Increasing $t_c$ to 3 years may not be economically worthwhile since the resulting increase in Y/R is only 6 g. Such a move however, would protect 2-year-old fish that are spawning for the first time. Because of the flattening of the yield curves at high $F$ values, the effect of overexploitation on yield is small. However, the effects of overexploitation on recruitment is unknown, and requires future study.

## Acknowledgments

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# Reproduction, Growth, and Mortality of Red Drum *Sciaenops ocellatus* in Florida Waters

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**Abstract.**—Commercial and recreational catches of red drum *Sciaenops ocellatus* were sampled from Tampa Bay and Mosquito/upper Indian River Lagoon, Florida, between August 1981 and March 1983. Males matured at smaller sizes and younger ages than did females. Males matured when they were 350–799 mm FL (ages 1–3), and females matured when 550–899 mm (ages 3–6). In 1981 and 1982, red drum spawned between August and November, with peak spawning occurring in September–October. Histological evidence suggested that spawning occurred in nearshore Gulf of Mexico waters, in passes, and in the estuary. Ages determined from thin sections of otoliths were validated by length-frequency and marginal-increment analyses for fish ages 1–3 and by observations of oxytetracycline-marked fish for ages 5, 12, 16, and 18. Growth was rapid through age 4 or 5 but then slowed markedly. Growth rates of males and females were similar on each coast. Estimates for the von Bertalanffy growth equation parameters $K$ and $t_0$ were not significantly different between coasts; however, $L_\infty$ was significantly greater on the Atlantic coast. Therefore, predicted lengths of Atlantic fish were greater at all ages. Maximum observed lengths were 980 mm on the Gulf coast and 1110 mm on the Atlantic coast. Maximum observed ages of sampled fish were 24 years on the Gulf coast and 33 years on the Atlantic coast. The range of 95% confidence intervals for estimates of total annual mortality rate on the Gulf coast was 87–98% for ages 2–4; on the Atlantic coast, the range was 50–76% for ages 2–6.

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The red drum *Sciaenops ocellatus* is an estuarine-dependent sciaenid found in nearshore waters (usually <22 m deep) from northern Mexico to Massachusetts (Yokel 1966, Lux and Mahoney 1969, Ross et al. 1983); it is occasionally found north of Chesapeake Bay (Yokel 1980). Red drum support important recreational and, until recently, commercial fisheries in most coastal areas of the U.S. south Atlantic and Gulf of Mexico (Mercer 1984). These fisheries have recently undergone strict management in Florida to reduce growth and recruitment overfishing (Swingle et al. 1984, Goodyear 1987).

Despite the importance of the red drum, little is known about its life history in Florida. While the spawning season and size at maturity have been described for red drum in Texas (Pearson 1929, Miles 1951, Matlock 1985) and Mississippi (Overstreet 1983), the spawning season in Florida has been inferred only from larval collections taken along the Gulf coast (Springer and Woodburn 1960, Yokel 1966, Jannke 1971, Peters and McMichael 1987). Age and growth have been described for juvenile and adult red drum in U.S. south Atlantic waters (Bearden 1967, Theiling and Loyacano 1976, Music and Pafford 1984, Daniel 1988) and in the northern and western Gulf of Mexico (Pearson 1929; Simmons and Breuer 1962; Rohr 1964, 1980; McKee 1980; Doerzbacher et al. 1988). In Florida, larval and juvenile age and growth have been studied in Tampa Bay (Peters and McMichael 1987), but only limited data are available on early growth in other areas (Kilby 1955, Roessler 1967).

This paper describes reproduction, age, growth, and mortality for red drum on the Gulf and Atlantic coasts of Florida. Weight-length and length-length relationships are also presented.

## Methods and materials

From August 1981 through March 1983, monthly samples of red drum were collected from commercial and recreational catches in two coastal areas of Florida: (1) Tampa Bay (27° 40′N, 82°35′W) on the Gulf coast, and (2) Mosquito/upper Indian River Lagoon (28°40′N, 80°40′W) on the Atlantic coast. Fish were captured using a variety of gear, including trammel nets, gill nets, hook-and-line, and haul seines. Fork length (FL) in millimeters was measured on all fish in the catch. Each month on both coasts, a random subsample was taken, and up to ten fish per length interval (<300, 400–499, 500–699, 700–899, and >899 mm) were measured for total length (TL) and standard length (SL), weighed for whole weight (W) to the nearest ounce (later converted to grams), and sampled for gonads and otoliths (sagittae). Gonads were preserved in the field in Davidson's or Zenker's fixative (Humason 1972), soaked in water for 24 hours in the laboratory, and then stored in 70% ethanol. A

**Table 1**
Reproductive classes of red drum gonads of each sex.

| Class | Female | Male |
|---|---|---|
| 1. **Immature** | Few folds of ovigerous lamellae; few or no primary oocytes; oogonia predominate; diameter of ovary <3.0 mm. | Only spermatogonia present; no evidence of tubule development. |
| 2. **Developing** or **Resting virgin** | Ovigerous lamellae fill lumen of entire gonad; abundant primary oocytes; oogonia present at periphery of lamellae. Lamellae contain abundant primary oocytes; few, if any, oogonia present; absence of atretic oocytes; tunica thickened. | Early spermatogenesis; few scattered cysts of primary spermatocytes; peripheral tubules differentiating lumen not developed. |
| 3. **Maturing** | Early vitellogenesis; oogonia, primary oocytes, and oocytes with yolk vesicle present. | Mid-spermatogenesis; spermatogonia, cysts of spermatocytes and a few spermatids present along tubules. |
| 4. **Mature** | Late vitellogenesis; oogonia, primary oocytes, and oocytes with yolk vesicles and yolk globules present. | Late spermatogenesis; few spermatogonia; spermatozoa collecting in tubules and central lumen. |
| 5. **Gravid** | Maturation. Oogonia, primary oocytes and oocytes with yolk vesicles, globules, and migrating nuclei present. | Reduced number of spermatogenic cysts; efferent ducts filled with spermatozoa; lumen of central duct partially filled with spermatozoa. |
| 6. **Spawning** or **Partially spent** | Amorphous, hydrated oocytes present; oogonia, primary oocytes, and oocytes with yolk vesicles, yolk globules, and migrated nuclei present; fragments of ruptured oocytes scattered throughout; collapsed, empty follicles present; yolk remnants usually present in connective tissue and lamellae; tunica greatly thickened. | Efferent ducts filled with spermatozoa; spermatozoa in main collecting duct; distal portions of a few efferent tubules empty and somewhat thickened; spermatogonia absent. |
| 7. **Spent** | Oogonia and primary oocytes present in budding ovigerous lamellae; ovary with "empty" areas; "plugs" of unshed oocytes present; atretic oocytes scattered throughout, usually in association with blood vessels. | No spermatogonia or spermatocytes present; efferent tubules empty; lumen of central collecting duct with few sperm; testis greatly reduced in size; tunic of previous spawners thickened and convoluted. |
| 8. **Recovering** | Prolific recrudescence of ovigerous lamellae with myriad oogonia and primary oocytes; only gamma and delta atretic oocytes present in the lamellae. Tunica thickened and convoluted. | Network of efferent tubules lined with spermatogonia; numerous PAS leucocytes present in central sinus; tunica thickened and convoluted. |

6-mm-thick sample from the central portion of one lobe of each gonad was embedded in paraffin, sectioned to 6-μm thickness, stained with Mayer's haematoxylin (Humason 1972) and eosin Y, and mounted for microscopic examination. Additionally, sections of vitellogenic ovaries fixed in Zenker's fluid were sectioned to 8-μm thickness and stained with Heidenhain's azan (Humason 1972).

Eight classes of maturity (Table 1) were distinguished based on the histological criteria of Wallace and Selman (1981) and Hunter and Macewicz (1985) for oogenesis and Grier (1981) and Grier et al. (1987) for spermatogenesis. Recognition of oocyte atresia and rejuvenation was important in determining whether a fish had previously spawned. Atretic oocytes were recognized by degeneration of the zona radiata, nuclear membrane, and yolk globules (Moe 1969, Wallace and Selman 1981, Hunter and Macewicz 1985). "Rejuvenation" is defined as the development of oocytes that were held in an advanced perinuclear stage of development since the previous spawning season. These clutches of oocytes in postspawn, recovering females exhibited a characteristic dual cytoplasmic banding (Yamamoto 1956, Howell 1983).

Length at maturity was determined by grouping fish by coast and sex into 50-mm intervals, determining the percentage that were mature (≥ class 4) within each interval, and estimating the length at which 50% of the fish were mature by interpolating between interval midpoints. Oocyte diameters, measured with an ocular micrometer, were used to define the spawning season. Only oocytes whose nuclei were included in the cross section were measured, because these have been shown to represent true oocyte diameters (Foucher and

Beamish 1980). A total of 100 oocytes in a randomly chosen lamella were measured in each female gonad to calculate mean oocyte diameters within subsamples. To further delineate the spawning season and characterize variation in egg size, ten of the largest oocytes from each section were also measured (DeMartini and Fountain 1981), and their mean was plotted against the collection date.

Otoliths were excised from subsampled fish, cleaned, and stored dry in vials. Sagittae were sectioned in the laboratory using a Beuhler Isomet Low-Speed Saw with diamond wafering blades. A 0.5-mm-thick section, cut through the core of the right sagitta, was mounted on a microscope slide with Coverbond Mounting Media. Each section was examined for age marks using a dissecting scope (32×) with reflected light. All sections were independently read once by two individuals; then, when necessary, a common reading was conducted. Determining age by simply counting annuli was not always possible because annulus formation occurs about 2–6 months after the anniversary of the actual hatching date (see "Age Determination and Growth" section). To assign ages accurately, we assumed a biologically realistic hatching date of 1 October (see "Spawning Size, Age, Season, and Location" section; Matlock 1984), and ages were incremented on this date. Observations of otolith sections from oxytetracycline (OTC)-marked fish served to directly validate opaque bands as annuli. Oxytetracycline-injected fish (intramuscular injection of 25 mg/kg body wt.) were held in outdoor ponds ($n = 4$) for subsequent recapture and examination after they were free for more than 1 year. All four fish were recaptured after 19 months.

Red drum captured by all gear types were included in the growth analyses. The von Bertalanffy (1957) growth equation, $FL = L_\infty (1 - \exp[-K(t - t_0)])$, was fit to observed age-length data by using the NLIN procedure (Marquardt option) of SAS (Vaughan and Kanciruk 1982). Growth equation parameters are defined as follows: $L_\infty$ = the average fork length (mm) that a fish would achieve if it were allowed to grow indefinitely in accordance with the model; $K$ = Brody's growth constant; $t_0$ = the hypothetical age at which a fish would have zero length, and $t$ = age in years (Ricker 1975). The weight-length relationship was described by linear regression of $\log_{10}$-transformed data. Analysis of covariance was used to test for differences between regressions.

Age-length keys were applied to length frequencies to separate age groups and develop sample abundance data used to estimate total annual mortality rate ($A$): $A = 1 - S$, where $S$ is the annual survival rate. Age-length keys were developed for each season for combined samples captured by trammel net, hook-and-line, and haul-seine. Abundance of each age-group in the samples was then summed over all seasons during the study period. Total annual mortality rates were estimated from truncated age data that included all fully recruited age-groups with sample abundance of five or more fish. This procedure eliminated any bias inherent in the collection of large fish (Chapman and Robson 1960). Survival rates were calculated using the modified Heincke method (Seber 1973), Robson and Chapman (1961) estimates developed for truncated age data, and catch curves.

## Results and discussion

### Spawning size, age, season, and location

Males matured at smaller sizes ($\chi^2$-test, $p<0.05$) and younger ages than did females on both coasts. Some Gulf coast males were sexually mature after they reached 400 mm, and some on the Atlantic coast were mature after they reached 350 mm (Table 2). Interpolated lengths at 50% maturity were 529 mm and 511 mm, respectively. Most males were mature at age 1 or 2, and all were mature by age 3 (see "Age Determination and Growth" section). Some Gulf coast females were sexually mature after they reached 600 mm, and some on the Atlantic coast were mature after they reached 550 mm. Lengths at 50% maturity were 825 and 900 mm, respectively. Some females were mature at age 3, and all were mature by age 6.

While results of previous investigations suggest that the size and age at which red drum mature may vary over its geographical range (Pearson 1929, Gunter 1950, Miles 1951, Overstreet 1983, Music and Pafford 1984), we show that there are also large maturational differences between sexes. Lengths at 50% maturity were about 300–390 mm smaller for males than females. In Mississippi, males and females began developing when they were 300–549 mm SL (358–629 mm FL); however, only after growing to 700 mm SL (792 mm FL) were more than 50% of the samples of either sex mature (Overstreet 1983). Female red drum in Texas matured during their fourth or fifth year, at about 750–850 mm TL (711–803 mm FL) (Pearson 1929, Miles 1951, Matlock 1985). A 755-mm TL (716 mm FL) male red drum sampled in Georgia had well-developed gonads and was apparently mature (Music and Pafford 1984).

Spawning peaked on both coasts of Florida from about September through October. Maximum oocyte diameters and the presence of eggs with yolk vesicles, globules, and migrating nuclei indicated that active

Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

**Table 2**

Percent of sampled red drum in each 50 mm FL length interval that were mature (≥ class 4) on the Gulf and Atlantic coasts of Florida. Numbers in parentheses are numbers of fish examined.

| Fork length (mm) | Gulf | | Atlantic | |
|---|---|---|---|---|
| | Male | Female | Male | Female |
| 200–249 | | 0 (3) | | |
| 250–299 | 0 (7) | 0 (4) | 0(10) | 0 (7) |
| 300–349 | 0(21) | 0(17) | 0 (7) | 0(17) |
| 350–399 | 0(18) | 0(24) | 9(22) | 0(22) |
| 400–449 | 16(19) | 0(16) | 16(19) | 0(32) |
| 450–499 | 24(21) | 0(24) | 35(20) | 0(28) |
| 500–549 | 47(19) | 0 (6) | 56(25) | 0(18) |
| 550–599 | 81(27) | 0(24) | 70(20) | 7(15) |
| 600–649 | 88(43) | 2(53) | 85(20) | 0(26) |
| 650–699 | 85(36) | 4(28) | 82(38) | 0(18) |
| 700–749 | 100(36) | 28(36) | 93(27) | 0(36) |
| 750–799 | 100 (6) | 36(14) | 94(17) | 7(14) |
| 800–849 | 100 (3) | 50 (2) | 100 (6) | 7(14) |
| 850–899 | 100 (1) | 100 (3) | 100 (4) | 0 (1) |
| 900–949 | 100 (6) | 100 (3) | 100 (1) | 100 (1) |
| 950–999 | 100 (2) | 100 (2) | 100 (2) | 100 (9) |
| 1000–1049 | | 100 (1) | 100 (1) | 100 (5) |
| 1050–1099 | | | 100 (2) | |
| 1100–1149 | | | | 100 (1) |

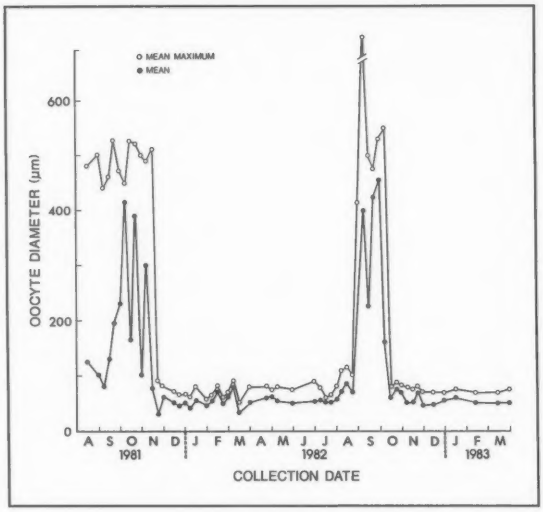



**Figure 1**

Mean and mean maximum oocyte diameters for red drum sampled from both Atlantic and Gulf coasts of Florida.

vitellogenesis occurred in August and September 1981, when the study began on the Gulf and Atlantic coasts, respectively (Fig. 1). Gonads were in spawning condition or were partially spent during September–October 1981. In 1982, active vitellogenesis began in August, and most spawning or partially spent individuals were collected in September. Mean and maximum oocyte diameters declined by mid-November 1981 and by mid-October 1982, indicating cessation of peak spawning (Fig. 1).

These results are consistent with the findings of previous studies (Pearson 1929, Mansueti 1960, Yokel 1966, Jannke 1971, Sabins 1973, Peters and McMichael 1987). However, spawning in Tampa Bay may have begun earlier than August in 1982 because larval and juvenile length-frequency distributions and otolith analyses of daily growth indicated that spawning had begun in mid-July (Peters and McMichael 1987). Apparently, spawning in mid-July did not occur in a large enough portion of the population to be reflected in our samples. Macroscopic analyses of adult gonads and analyses of gonosomatic indices have suggested that spawning takes place in Texas during October through February (Heffernan 1977) and that spawning off Mississippi takes place during summer (Overstreet 1983).

Ovarian histological features provided evidence that spawning occurs in the nearshore Gulf of Mexico, in the vicinity of passes, and within estuaries. Ovaries of females captured in all three areas displayed either (1) advanced oocytes with migrating nuclei or hyaline oocytes released from the follicular layer, indicative of an imminent spawn (DeMartini and Fountain 1981), or (2) atretic bodies and postovulatory follicles (POF), indicative of a recent spawn (Yamamoto and Yoshioka 1964, Takita et al. 1983, Hunter and Macewicz 1985). A female captured 4.8 km off the Florida Gulf coast had numerous oocytes with migrating nuclei, and a male from the same site had spermatozoa filling the efferent duct of the testes, both of which suggest imminent offshore spawning. A large female red drum captured about 7 km within the mouth of Tampa Bay contained ovulated hydrated oocytes, POF, and several atretic oocytes. All of these artifacts indicate that she had recently spawned. Supporting the hypothesis that estuaries are also used as spawning sites is the fact that females ($n = 4$) that had POF or hyaline oocytes released from the follicle layer were found about 42 km within Tampa Bay, 35 km south of Ponce de Leon Inlet in Mosquito Lagoon, and 90 km north of Sebastian Inlet.

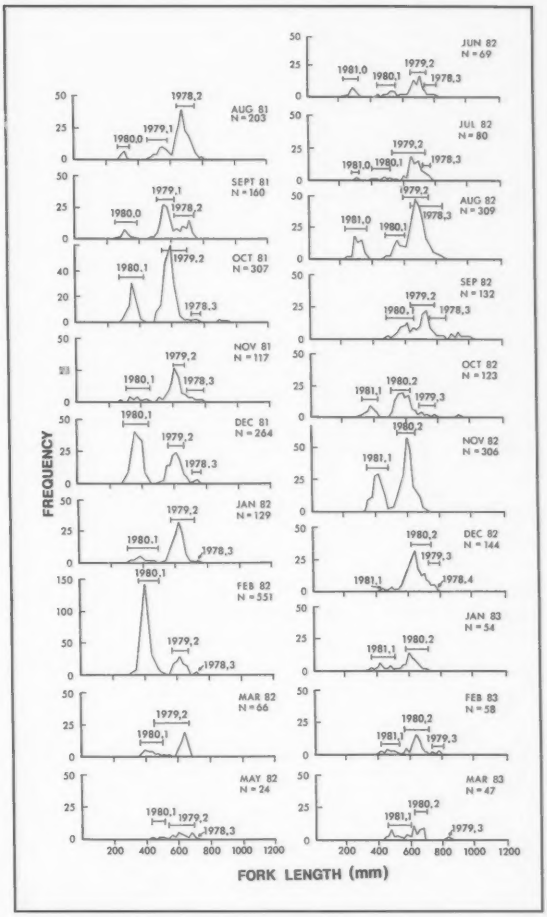
Based on data from egg and larval collections made just inside passes, most investigators have concluded that red drum spawn principally in nearshore areas close to channels and passes (Pearson 1929, Miles 1950,

Simmons and Breuer 1962, Yokel 1966, Jannke 1971, Holt et al. 1985). Our data suggest that spawning may also occur over the nearshore continental shelf and in estuaries. Collections of mature or recently spent fish made in nearshore Gulf waters from just outside the barrier islands to depths of 69.5 m suggest that spawning takes place offshore in the Gulf of Mexico (Christmas and Waller 1973; Heffernan 1977; W.A. Fable, NMFS Panama City Lab., Drum seine observers trip report, 18–21 Aug. 1982. Memo 00.Sep.82*002148 to A.C. Jones, NMFS Miami Lab., 4 p.). Peters and McMichael (1987) reported that although most spawning in Tampa Bay occurred close to its mouth, some spawning probably took place in nearshore Gulf waters. Recent egg collections provide evidence that red drum spawn within Mosquito Lagoon (Johnson and Funicelli In press). Our collection of females in Mosquito Lagoon containing POF corroborate these findings and suggest that red drum found equally far within Tampa Bay may also be spawning within the estuary. Moreover, red drum movement was observed during a sonic tracking study in Mosquito Lagoon (Carr and Smith 1977, Carr and Chaney 1976) and little directed movement during the spawning season was noted.

## Age determination and growth

Ages of red drum from 0 to at least 18 could accurately be determined using otoliths. Red drum sagittae showed clearly delineated, easily interpreted (100% agreement between counts) hyaline and opaque bands. Otoliths with 0–33 opaque bands were examined; they were taken from 1085 red drum (551 Gulf coast and 534 Atlantic coast) with size ranges of 225–1110 mm. Although ages of red drum were validated for only the first 18 years, we assumed, for age and growth analysis, that each opaque band represents an annual mark (annulus).

Minimally overlapping monthly length frequencies, a consistent marginal increment minima each year, and observations of oxytetracycline-injected fish supported the hypothesis that the opaque bands are annuli. Modal length progressions representing the 1978, 1979, 1980, and 1981 year-classes on the Gulf coast and 1980 and 1981 year-classes on the Atlantic coast could be followed in length frequencies (Figs. 2, 3). These length modes could be followed for fish up to 3 years-old and consistently agreed with lengths of fish having corresponding otolith-determined ages. The periodicity of the mean monthly marginal increment minima each winter (December–March) for fish having one or two opaque bands further suggests that opaque bands were deposited annually (Fig. 4). Opaque bands on fish older than age 3 are also probably annuli. Four adult red drum that were injected and held in outdoor ponds for 19 months deposited one opaque band each between release (August 1986) and recapture (March 1988). These fish were 5, 12, 16, and 18 years-old when recaptured.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FORK LENGTH (mm)
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SEPT 81 N = 160
OCT 81 N = 307
NOV 81 N = 117
DEC 81 N = 264
JAN 82 N = 129
FEB 82 N = 351
MAR 82 N = 66
MAY 82 N = 24
JUN 82 N = 69
JUL 82 N = 80
AUG 82 N = 309
SEP 82 N = 132
OCT 82 N = 123
NOV 82 N = 306
DEC 82 N = 144
JAN 83 N = 54
FEB 83 N = 58
MAR 83 N = 47

**Figure 2**

Monthly length frequencies for red drum from the Gulf coast of Florida. No collections were made in April 1982. Horizontal bars show length ranges for otolith-aged year-classes and are labeled for year-class and age in years.

Otoliths have been used to determine the age of red drum (Miles 1951, Rohr 1964, Theiling and Loyacano 1976), but the use of opaque bands as an age determinant has never been adequately tested. Off Mississippi, annuli apparently form on otoliths during winter or spring (Rohr 1964). In Texas, where the validity of using scales to determine ages of red drum ≤4.5 years-old has been established (Matlock et al. 1987), annuli form on scales between February and April in

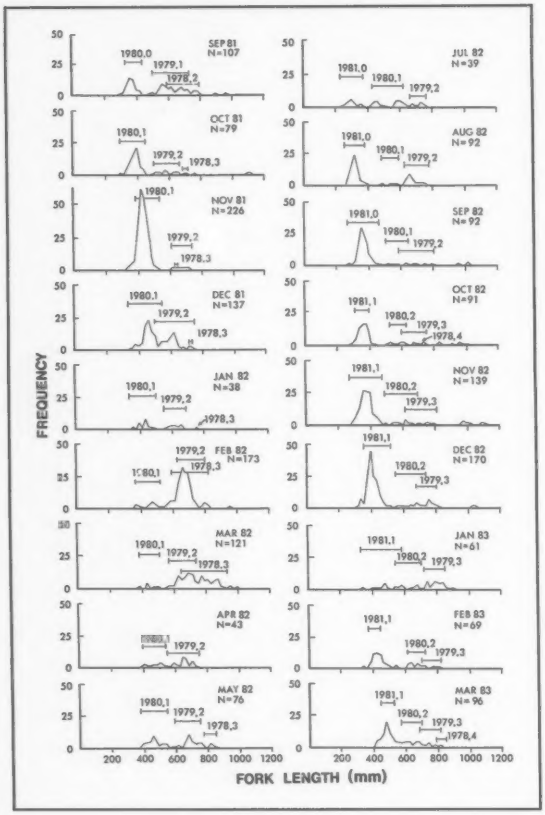


**Figure 3**

Monthly length frequencies for red drum from the Atlantic coast of Florida. No collections were made in June 1982. Horizontal bars show length ranges for otolith-aged year-classes and are labeled for year-class and age in years.

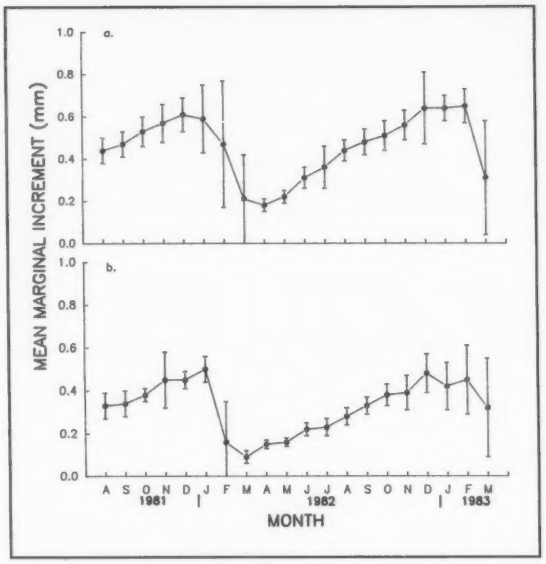


**Figure 4**

Mean monthly marginal increment (±1 SD) for red drum in Florida waters with (a) one and (b) two annuli on otolith sections. Differences between coasts were not significant (ANOVA, $p>0.05$), therefore pooled data are presented.

Matagorda Bay (Wakefield and Colura 1983), during winter in Aransas/Corpus Christi Bay (Pearson 1929), and as early as January in all Texas bays (Matlock et al. 1987). Red drum deposit a first annulus on otoliths and scales during their second winter, when they are about 14–18 months-old (Pearson 1929, Rohr 1964, Theiling and Loyacano 1976, Hysmith et al. 1983, Wakefield and Colura 1983, Matlock 1984, Matlock et al. 1987). Apparently, juvenile red drum that measure 40–100 mm during their first winter (Kilby 1955, Peters and McMichael 1987) do not form an annulus; our smallest specimen with an annulus was 379 mm.

Red drum grew rapidly until age 4 or 5, and then growth slowed markedly (Table 3; Fig. 5). For each coast, the average observed sizes of fish ages 1–3 were not significantly different between sexes (Student's $t$-test; $p>0.10$ in all cases). However, in comparing coasts, the average observed sizes were significantly larger ($p<0.001$) at ages 1 and 2 on the Atlantic coast than they were on the Gulf coast. After age 2, growth appeared to be slower on the Atlantic coast; however, the variance for age 3 lengths was significantly greater ($F$-test; $p<0.05$) on the Atlantic coast. Sample sizes of older age groups were too small to test for statistical differences.

Lengths predicted from the von Bertalanffy growth curve agreed with the average observed lengths of red drum on the Gulf and Atlantic coasts (Table 3; Fig. 5). Asymptotic length ($L_\infty$) was significantly larger (Student's $t$-test, $p<0.01$) on the Atlantic coast than on the Gulf coast, while the Brody's growth constant ($K$) and age at zero length ($t_0$) were not significantly different ($p>0.05$). Therefore, predicted lengths were greater at all ages for Atlantic coast red drum than for Gulf coast fish. Our estimates of asymptotic length are generally greater than other reported values: 717 mm TL (680 mm FL), 835 mm TL (789 mm FL), and 803 mm TL (760 mm FL) for Lower Laguna Madre, Matagorda, and Galveston Bays in Texas, respectively (Wakefield and Colura 1983); 918 mm TL (865 mm FL) in Texas bays (Doerzbacher et al. 1988); and 950 mm TL (894 mm FL) in Mississippi Sound (Rohr 1980). This suggests that red drum grow larger in Florida or, as

**Table 3**
Average observed and predicted fork lengths (mm) for red drum sampled from Gulf and Atlantic coasts of Florida. Sample sizes are in parentheses.

| | Gulf | | Atlantic | |
|---|---|---|---|---|
| Age (yr) | Average observed | Predicted | Average observed | Predicted |
| 0 | 296 (62) | | 335 (59) | |
| 1 | 436(169) | 337 | 462(192) | 373 |
| 2 | 635(232) | 557 | 655(166) | 581 |
| 3 | 736 (65) | 696 | 742 (66) | 718 |
| 4 | 845 (5) | 784 | 768 (14) | 808 |
| 5 | 877 (1) | 839 | 863 (5) | 867 |
| 6 | | 874 | 871 (5) | 905 |
| 7 | | 896 | | 931 |
| 8 | | 910 | 995 (2) | 948 |
| 9 | 975 (1) | 919 | 973 (2) | 959 |
| 10 | | 925 | 986 (1) | 966 |
| 11 | | 928 | 918 (1) | 971 |
| 12 | 925 (1) | 930 | 894 (1) | 974 |
| 13 | | 932 | | 976 |
| 14 | | 933 | 1028 (2) | 977 |
| 15 | | 933 | 954 (1) | 978 |
| 16 | | 933 | 960 (1) | 979 |
| 17 | 968 (1) | 934 | | 979 |
| 18 | 898 (2) | 934 | | 979 |
| 19 | 957 (1) | 934 | 975 (1) | 979 |
| 20 | | 934 | | 980 |
| 21 | 918 (1) | 934 | | 980 |
| 22 | 960 (6) | 934 | 1110 (1) | 980 |
| 23 | | 934 | | 980 |
| 24 | 980 (1) | 934 | | 980 |
| 25 | | | 1038 (3) | 980 |
| 26 | | | 1060 (1) | 980 |
| 27 | | | | 980 |
| 28 | | | 983 (2) | 980 |
| 29 | | | | 980 |
| 30 | | | | 980 |
| 31 | | | | 980 |
| 32 | | | | 980 |
| 33 | | | 1050 (1) | 980 |

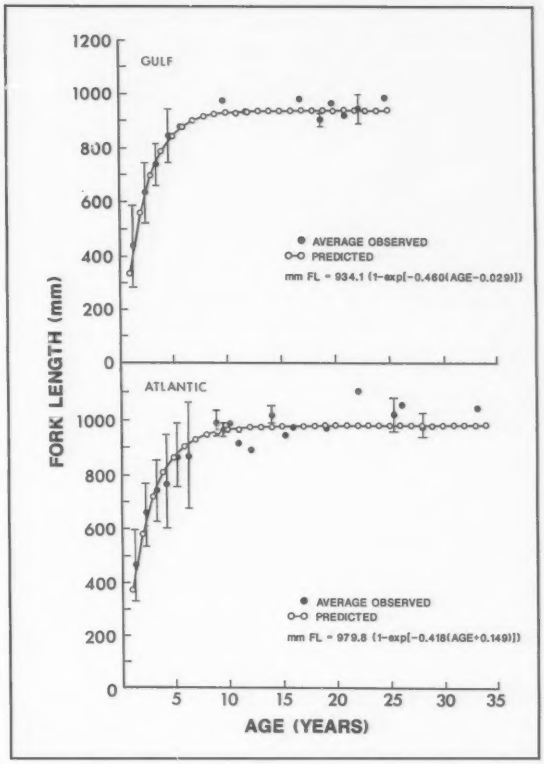


**Figure 5**
Average observed (±2 SD or range if $n = 2$; see Table 3) and predicted mean lengths of red drum in Florida waters.

noted by Matlock (1984), that the larger fish which predominately inhabit continental shelf waters were not adequately sampled in Texas and Mississippi. Matlock (1984) estimated the von Bertalanffy growth equation for red drum in Texas using data from Pearson (1929) and found what he considered a more reasonable estimate of $L_\infty$ of 1068 mm TL (1002 mm FL).

Length-at-age estimates of red drum in Florida were similar to those reported in past literature for red drum in Texas (Pearson 1929, Miles 1951, Simmons and Breuer 1962; Table 4). However, red drum in Florida appear to grow more rapidly than red drum in Mississippi (Rohr 1980), South Carolina (Thieling and Loyacano 1976), and those in a more recent study from Texas (Wakefield and Colura 1983). However, as noted above the differences in length-at-age estimates could be attributed to a sampling bias toward smaller nearshore fish.

## Mortality

Ninety-five percent confidence limits for estimates of total annual mortality rate (1 – S) using sample abundance data ranged 87–98% for red drum ages 2–4 on the Gulf coast and 50–76% for red drum between ages 2–6 on the Atlantic coast during 1981–83. Red drum were fully recruited by age 2. Sample size of fish older than 4 years on the Gulf coast and 6 years on the Atlantic coast fell below the suggested lower limit of five fish to ensure unbiased estimates (Chapman and Robson 1960). Mean estimates of total annual mortality rates were consistently greater for Gulf coast fish (Table 5).

Total annual mortality of red drum has been estimated for Everglades National Park in Florida and for Texas bay systems. In Everglades National Park, Rago

**Table 4**

Literature accounts of mean fork lengths at age for red drum. Fork lengths are in millimeters and were converted from TL or SL, if necessary, using the relationships in text.

| | Age (yr) | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Area, study, and method | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| **Texas** | | | | | | | | | | |
| Pearson (1929) | | | | | | | | | | |
| Aransas/Corpus Christi Bays; length frequency | 300 | 530 | 630 | 750 | 840 | | | | | |
| Miles (1951) | | | | | | | | | | |
| Aransas Bay; otoliths | 380–423 | 575 | 630–684 | | | 826 | 871* | 917–940 | | |
| Simmons and Breuer (1962) | | | | | | | | | | |
| Lower coast; tag recapture | 322 | 519 | 693 | | | | | | | |
| Wakefield and Colura (1983) | | | | | | | | | | |
| Lower Laguna Madre; scales | 290 | 447 | 542 | | | | | | | |
| Matagorda Bay; scales | 255 | 399 | 526 | 605 | 660 | | | | | |
| Galveston Bay; scales | 275 | 439 | 547 | 619 | | | | | | |
| **South Carolina** | | | | | | | | | | |
| Theiling and Loyacano (1976) | | | | | | | | | | |
| otolith sections** | 429 | 560 | 695 | 782 | 803 | 842 | 803 | | | |
| **Mississippi** | | | | | | | | | | |
| Rohr (1980) | | | | | | | | | | |
| otoliths | 356 | 522 | 638 | 717 | 772 | 810 | 839 | 853 | 867 | 875 |
| **Florida** | | | | | | | | | | |
| Present study | | | | | | | | | | |
| Gulf coast; otolith sections | 337 | 557 | 696 | 784 | 839 | 874 | 896 | 910 | 919 | 925 |
| Atlantic coast; otolith sections | 373 | 581 | 718 | 808 | 867 | 905 | 931 | 948 | 959 | 966 |

*A mixture of fish age seven and eight.
**Average size for age group from June through November.

**Table 5**

Pooled mean estimates and 95% confidence intervals of total annual mortality (A) for red drum ages 2–4 on the Gulf coast and ages 2–6 on the Atlantic coast.

| | Total annual mortality | | | |
|---|---|---|---|---|
| | Gulf | | Atlantic | |
| Method | A | 95% CI | A | 95% CI |
| Seber (1973) | 0.92 | 0.91–0.94 | 0.65 | 0.59–0.70 |
| Robson and Chapman (1961) | 0.91 | 0.90–0.93 | 0.66 | 0.63–0.70 |
| Catch curve | 0.94 | 0.87–0.98 | 0.65 | 0.50–0.76 |

and Goodyear (1985) used tag-recapture days-at-large data to estimate a total annual mortality rate of 0.73 during 1984–85. Also based on tag-recapture data, total annual mortality rates in Texas bays were about 68% during 1976–77 (Matlock and Weaver 1979) and 80–87% during 1975–1979 (Green et al. 1985). Matlock (1984) estimated the total annual mortality rate to be 80% for all Texas bays during 1977–1981.

Apparent total annual mortality rates in Florida for red drum ages 2–6 are high, especially for a species that may live about 25–35 years. Theoretically, fish with such longevity (assuming constant mortality rate) would have a natural mortality rate of only about 12–18%; this rate allows for survival to the observed maximum ages (Royce 1972, Hoenig 1983). Our much greater estimates of total annual mortality for fish ages 2–6 may reflect one or more of the following: (1) a higher rate of natural mortality for younger fish (i.e., natural mortality is not constant), (2) high fishing-mortality rates within estuaries, and/or (3) emigration from estuaries (sampling area) before age 4 on the Gulf coast or age 6 on the Atlantic coast. In the first two cases, estimates of total mortality are unbiased, although component parts (fishing and natural mortality) are not the same. In the third case, total annual mortality would be overestimated because older fish that left the sampling area would be underrepresented in the catch.

While data for evaluating whether natural mortality changes with age are not available, tag-recapture data suggest that fishing mortality is high and that emigration does occur. Annual tag-return rates of

**Table 6**
Weight-length regressions of red drum sampled from the Gulf and Atlantic coasts of Florida. W = weight (g); FL = fork length (mm).

| Area | $N$ | FL (mm) | $a$ (1 SE) | $b$ (1 SE) | $r^2$ |
|---|---|---|---|---|---|
| Gulf | 491 | 242–1000 | $6.1673 \times 10^{-6}$ ($0.4301 \times 10^{-6}$) | 3.0984 (0.0114) | 0.993 |
| Atlantic | 484 | 257–1110 | $9.3993 \times 10^{-6}$ ($0.6616 \times 10^{-6}$) | 3.0275 (0.0115) | 0.993 |

70–80% occurred in southwest Florida during the 1961–65 Schlitz Tagging Programs, and the average tag-return rate throughout the state was 46% (Beaumariage 1969). More recent annual tag-return rates in Florida were 11–25% (Murphy and Taylor 1985) and 12% (Rago and Goodyear 1985), but if these are adjusted to account for a probable low tag-reporting rate, e.g., 36% in Texas (Green et al. 1983), then actual annual recapture rates in Florida could still be high: 31–69%. Limited data on the emigration of red drum suggest a little exchange from estuarine to nearshore waters. Subadult red drum tagging studies within Tampa Bay have shown that about 2–6% of recaptured red drum came from outside the Bay (Murphy and Taylor 1985); similar results (1.4%) were reported for the Texas coast (Osburn et al. 1982). Fishing effort and "catchability" of red drum are probably lower in nearshore waters than within the estuary, which could cause the rates of emigration to be underestimated.

### Weight-length and length-length relations

Weight-length regressions (Table 6) were not significantly different ($p>0.05$) between sexes on each coast,

| | | |
|---|---|---|
| Atlantic | | |
| slope | df = 1, 480 | F = 0.21 |
| elevation | df = 1, 481 | F = 0.34 |
| Gulf | | |
| slope | df = 1, 487 | F = 1.60 |
| elevation | df = 1, 488 | F = 1.32, |

although the slopes and elevations were different between coasts with sexes combined,

| | | |
|---|---|---|
| slope | df = 1, 971 | F = 18.96 |
| elevation | df = 1, 972 | F = 27.5. |

Predicted weights for subadult red drum were similar; e.g., the predicted weight of a 500-mm fish is about 1.4 kg on both coasts. However, adult red drum on the Gulf coast were heavier at a given length than they were on the Atlantic coast; e.g., a 900-mm fish weighs 8.8 kg on the Gulf coast and 8.3 kg on the Atlantic coast.

**Table 7**
Length-length regressions of red drum in Florida. TL = total length (mm); FL = fork length (mm); SL = standard length (mm). Sample fork length range for all regressions was 225–1110 mm.

| | | | $Y = a + bX$ | | |
|---|---|---|---|---|---|
| $Y$ | $X$ | $N$ | $a$ (1 SE) | $b$ (1 SE) | $r^2$ |
| FL | TL | 1074 | 23.9383 (0.6704) | 0.9162 (0.0011) | 0.999 |
| TL | FL | 1074 | −25.2080 (0.7600) | 1.0898 (0.0013) | 0.999 |
| TL | SL | 1075 | 10.3832 (0.8970) | 1.1829 (0.0017) | 0.998 |
| SL | TL | 1075 | −7.6225 (0.7689) | 0.8343 (0.0012) | 0.998 |
| FL | SL | 1075 | 32.8951 (0.6934) | 1.0850 (0.0013) | 0.998 |
| SL | FL | 1075 | −29.4619 (0.6738) | 0.9202 (0.0011) | 0.998 |

Length-length regressions show that total length and standard length increase more rapidly than fork length as fish get larger (Table 7). Total length is about 1% greater at 300 mm FL and 6% greater at 1000 mm FL. Standard length is 18% less than fork length at 300 mm FL but only 12% less at 1000 mm FL.

## Summary

The following are significant features of the life history of red drum in Florida: rapid growth through age 4 or 5, relatively early sexual maturation (total maturity by age 3–6), a discrete peak in spawning activity during September–October, a life span of up to about 35 years, and spawning grounds located in nearshore waters, in passes and inlets, and inside large estuaries. These characteristics and the apparently high rate of annual mortality for red drum ages 2–6 suggest that only a small portion of the population survives to reach maturity. However, this annual rate of mortality (disappearance) has a component of emigration that warrants investigation. Recent management measures enacted by the Gulf of Mexico Fishery Management Council and the Florida Marine Fisheries Commission have limited fishing on the spawning stocks and have reduced fishing pressure on the immature fish.

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# Contrast in Reproductive Style Between Two Species of Sandfishes (Family Trichodontidae)

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**Abstract.**—The sandfish family Trichodontidae is comprised of two species endemic to the boreal Pacific: *Arctoscopus japonicus* is a common demersal fish of commercial importance in the western area around northern Japan, while *Trichodon trichodon* is found in the eastern waters, from Alaska to California, although there is no fishery for this species. The two species share many similar reproductive features such as large demersal eggs of 3.3–3.5 mm diameter, moderate fecundities of 1000–2000 eggs, and peculiar spawning habits on rocky shores. However, there are striking contrasts in several reproductive and early-life-history traits: the shape of the egg mass is spherical in *A. japonicus* versus an irregular shape in *T. trichodon*; spawning substrate is mostly *Sargassum* spp. versus rock; incubation period is about 2 months versus nearly 1 year; and, at hatching, *T. trichodon* has precocious pectoral and caudal rays as well as preopercular spines. Despite these differences, larvae of both species appear in the spring season. These features are discussed in relation to the contrasting thermal regimes of the surface waters characteristic of each species. It is suggested that *A. japonicus* has a more derived reproductive style than *T. trichodon*, including a typical pattern of indirect ontogeny. The remarkable seasonal thermal events in Japanese coastal waters may be responsible for the notable abundance of *A. japonicus*.

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The family Trichodontidae is a small family of marine fishes endemic to the boreal Pacific comprised of two species, *Arctoscopus japonicus* (Steindachner) from the western Pacific around Japan and *Trichodon trichodon* (Tilesius) from the eastern Pacific, ranging from Alaska to California. As indicated by the common name "sandfishes," they typically lie partly buried in the bottom (Nelson 1984). Due to peculiar morphological and ecological features, they have been placed at various times in different groups of fishes such as the Percoidei (Matsubara 1963) and Blennioidei (Greenwood et al. 1966).

The biology of *A. japonicus* has been extensively studied because of its special importance to commercial fisheries in northern Japan and Korea (for review, see Ochiai and Tanaka 1986). For *T. trichodon*, however, information is only briefly documented in the literature (Fitch and Lavenberg 1975, Eschmeyer and Herald 1983), except for Marliave (1981) and Bailey et al. (1983) who reported the early life history in detail, and Allen and Smith (1988) who quantitatively illustrated aspects of its zoogeography.

These studies and our own observations, mostly in the northern Sea of Japan, enable us to compare life history traits of these fishes and to discuss probable life strategies associated with zoogeography. The notable fluctuation of the stocks of *A. japonicus* is also considered from the standpoint of comparative ecology.

## Comparison between *Arctoscopus japonicus* and *Trichodon trichodon*

### Distribution

The family Trichodontidae is restricted in distribution to the coastal boreal regions of the North Pacific between about 35°N and 60°N (Fig. 1). Although Schmidt (1950) reported the occurrences of *A. japonicus* from Akutan Bay and the vicinity of Sitka Island, in the Gulf of Alaska, these records seem questionable (Eschmeyer and Herald 1983). Perhaps these two species have distinct geographica ranges, separated by longitude 160–170°E. *Arctoscopus japonicus* occurs over an extensive area on the western side, including the offshore regions; it is extremely abundant in the Sea of Japan and the Pacific coast off Hokkaido, where catches amounted to $3.8 \times 10^4$ tons in 1968 (Ochiai and Tanaka 1986). *Trichodon trichodon* is an eastern Pacific form with a wider range from Kamchatka to southeast of San Francisco, California; there is no fishery for this species, but it is fairly common throughout the coastal waters (Hart 1973, Fitch and Lavenberg 1975, Eschmeyer and Herald 1983, Allen and Smith 1988).

Depth range is variable from the surface to about 400 meters in both species; however, the main life zones are slightly different for the two species. *Arctoscopus japonicus* in the Sea of Japan usually occurs at moderate depths of 200–300 m, with optimum

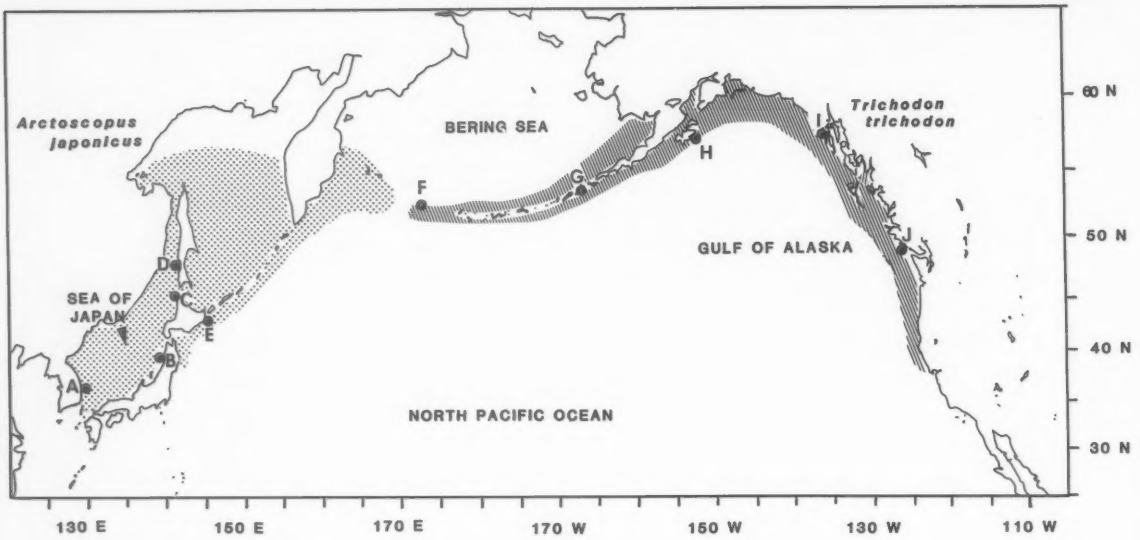


**Figure 1**

Geographical distribution of two species of sandfishes, family Trichodontidae. (A) Pohang, (B) Akita, (C) Wakkanai, (D) Kholmsk, (E) Nemuro, (F) Attu, (G) Dutch harbor, (H) Kodiak, (I) Sitka, (J) Vancouver. For references, see text.

temperature ranges of 2–5°C (Nishimura 1969). This zone is shifted to a shallower depth of 100–200 m on the Pacific side off Hokkaido (Ochiai and Tanaka 1986). During the spawning season, the adults move into water shallower than about 15 m. In contrast, *T. trichodon* is most frequent on the middle shelf at less than 150 m (Allen and Smith 1988) and spawning is restricted to the intertidal area.

## Reproductive ecology

Both species spawn large demersal eggs in rocky, shallow waters during winter months, but interesting ecological differences are found between them, summarized in Table 1. Typically, *A. japonicus* deposits a spherical egg mass tightly on *Sargassum* spp. in such a way that supporting stems pass through the axis of the mass. Successful deposition of secure substrata is of prime importance for survival of eggs, because egg capsules that detach from the substrata become stranded ashore and perish. Onset of spawning at fixed times and locations is characteristic of *A. japonicus*. In the Akita district, for instance, the onset of spawning at major spawning sites rarely fluctuates beyond 1 or 2 weeks from the end of November (Kato 1980).

In contrast, Eschmeyer and Herald (1983) reported that the eggs of *T. trichodon* are laid in a gelatinous mass attached to rocks. One report of a natural spawning was on the wall of a fully exposed surge channel

**Table 1**

Comparison between reproductive characters of *Arctoscopus japonicus* and *Trichodon trichodon* (after Ochiai and Tanaka 1986; Marliave 1981, unless otherwise indicated below).

| Characters | *A. japonicus* | *T. trichodon* |
|---|---|---|
| Spawning season | Mostly from the end of November to December | Around February |
| Spawning migration | Conspicuous | Indistinct |
| Spawning site; substrate | Coastal waters, 0–15 m depth; mostly *Sargassum* spp. | Intertidal waters, 0–1 m depth; rock |
| Shape of egg mass | Spherical, 3.3–7 cm in size | Irregular |
| Diameter of egg | 3.3–3.5 mm* | 3.52 ± 0.10 mm |
| Fecundity | 600–2300 | ~1000 |
| Incubation period | 56–78 days at 6°–9°C** | 1 year (?) at 8°–13°C |
| Synchronized hatching | No* | Yes; within 24 hours |

*Okiyama (unpubl.)
**Maekawa (1985); this indicates the most frequent period.

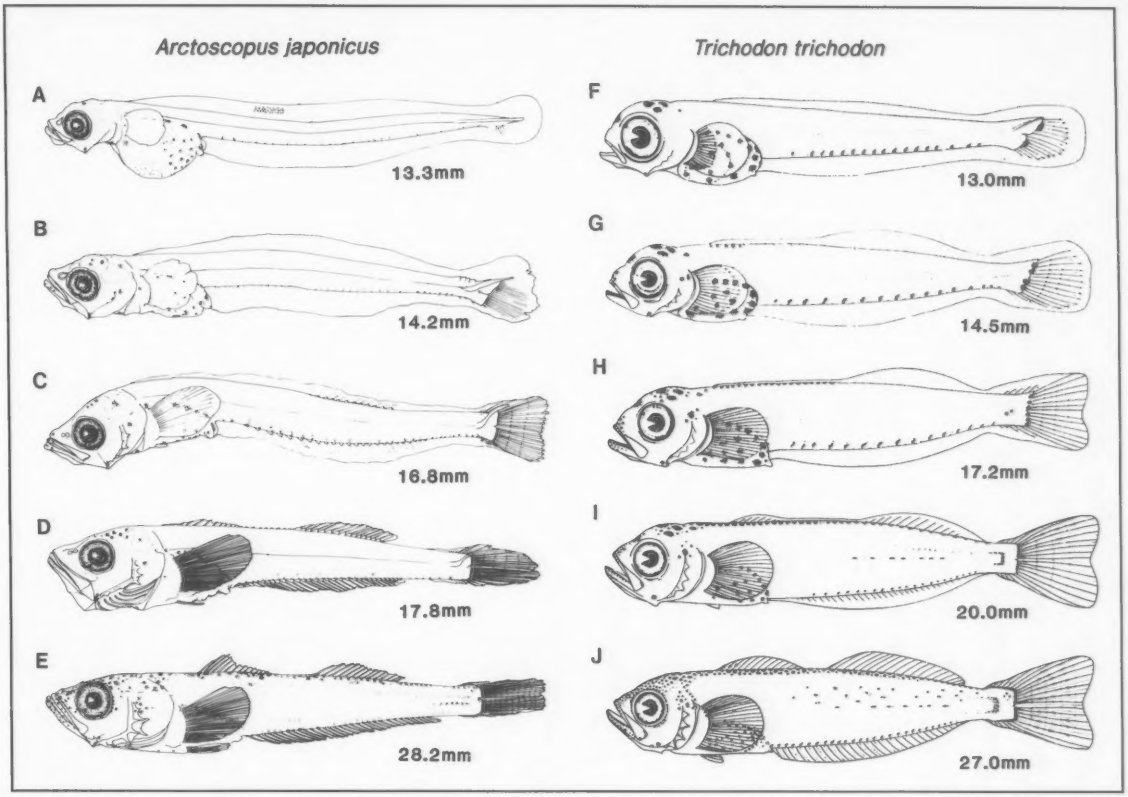


**Figure 2**

Comparison between early developmental stages of *Arctoscopus japonicus* (left) and *Trichodon trichodon* (right). Size in mm SL; preserved specimens (B–D after Okiyama 1988; F–J after Marliave 1981).

(Marliave 1981). It seems that *T. trichodon* selected this peculiar spawning location because it offered a refuge from egg predation as well as the high flow velocities necessary for respiration (Marliave 1981).

These contrasting reproductive styles should be associated with the different reproductive guilds proposed by Balon (1981, 1984). Although *A. japonicus* fits the "obligatory plant spawners" category, there is no guild relevant to *T. trichodon* within Balon's category of "nonguarders," suggesting its spawning habits may be unique.

## Early life history

Larvae and juveniles of both species have been described and illustrated in detail from field and/or laboratory-reared materials (Marliave 1981, Okiyama 1988). In Figure 2, a series of early developmental stages of these species is reproduced from these references, with additional specimens of *A. japonicus* included. Here, specimens of similar sizes are selected to facilitate interspecific comparison. The early growth of the two species is also compared in Figure 3, based on the laboratory-rearing results; the comparison reveals that *T. trichodon* is consistently larger than *A. japonicus* throughout the 2 months following hatching (Marliave 1981, Maekawa 1985). Despite close resemblances in the general morphology, there are remarkable differences in early developmental patterns between the two species. A few interesting aspects are as follows:

(a) Newly hatched larvae of *A. japonicus*, 13 mm notochord length (NL), are less advanced than those of *T. trichodon*, 13.0 mm standard length (SL); the body is slender, the notochord tip is straight, and fin elements, except several incipient caudal rays, and teeth are absent. In contrast, *T. trichodon* possesses many precocious characters, including a flexed notochord with full complement of principal caudal rays, developing pectoral rays and preopercular spines, in addition to a deeper body, larger eyes, and the presence of

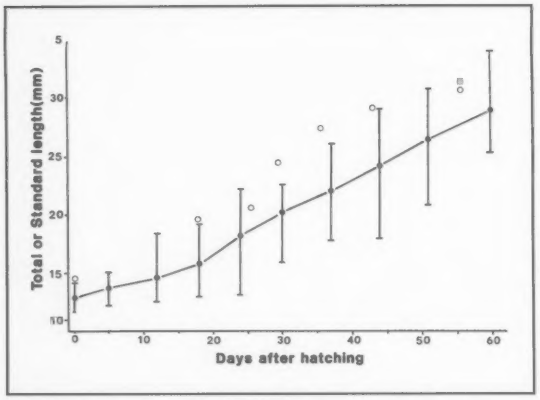


**Figure 3**
Early growth of laboratory-reared specimens of sandfishes in fresh condition. For *Arctoscopus japonicus*, average (●) and ranges (line) are shown in TL mm (after Maekawa 1985); for *Trichodon trichodon*, individuals (O) are shown in SL mm (after Marliave 1981).

**Table 2**
Comparison between fin formation of *Arctoscopus japonicus* and *Trichodon trichodon* (mm SL).

| | *A. japonicus** | | *T. trichodon*** | |
|---|---|---|---|---|
| Characters | start | finish | start | finish |
| 1st dorsal | 16.2 | 19.0 | 20.0– | 28.0 |
| 2nd dorsal | 16.2 | 17.8 | 20.0 | 27.0 |
| Anal fin | 16.2 | 17.8 | 20.0 | 27.0 |
| Pectoral | 14.9 | 17.8 | 13.0 | 17.2 |
| Pelvic | 16.8 | 19.0 | 27.0 | 30.0 |
| Caudal (principal) | 14.9 | 14.9 | 13.0 | 13.0 |

*Original data from specimens of the Sea of Japan.
**After Marliave (1981), slightly modified on the basis of two newly hatched larvae (13.0, 13.2 mm SL; preserved) provided by him.

teeth on both jaws. It is clear that these precocious characters are mostly concerned with active swimming. Fast swimming, coupled with large sizes, would not only facilitate successful feeding, but would play an effective role in lowering predation pressure. Slight but distinct size and development differences at hatching between the two species, therefore, are among the most important aspects of their early life histories.

(b) Orders of fin ray ossification of the two species can be derived from Table 2, although the available size series of *T. trichodon* (Marliave 1981) is somewhat limited. Except for the precocious caudal and pectoral fins in *T. trichodon*, all other fin meristics are formed in smaller specimens of *A. japonicus*. The entire size ranges for fin development are 14.9–19.0 mm in *A. japonicus* versus 13.0–30.0 mm in *T. trichodon*. Possible sequence of fin ossification is caudal-pectoral-anal-2nd dorsal-1st dorsal-pelvic for both species.

(c) Larvae of both species are sparsely pigmented and lack extensive melanin on the lateral side of the tail. Pigmentation is generally heavier in *T. trichodon* than in *A. japonicus*. In particular, earlier development of distinct spots along the anterior dorsal margin of *T. trichodon* is remarkable because this character first occurs after transformation into juveniles in *A. japonicus*.

(d) According to the conventional definitions of early developmental stage, transformation from larval to juvenile stages occurs at about 20 mm in *A. japonicus* versus about 30 mm in *T. trichodon*. However, *T. trichodon* is distinctly more advanced than *A. japonicus* in every early-life-history trait, except formation of fins other than the caudal and pectoral.

Major contrasts in their ontogenetic properties may be summarized as follows: *A. japonicus* has a distinct, but truncated, metamorphosing phase (20–30 mm SL) closely corresponding to the change from pelagic to demersal life (Minami and Tanaka 1985, Okiyama unpubl.); in contrast, *T. trichodon* has a less distinct metamorphosing phase (30–50 mm SL) without any ecological shifts other than possible decrease of schooling tendencies (Marliave 1981, Bailey et al. 1983), although it starts burying itself in the sand at 55–60 mm SL (J.B. Marliave, Vancouver Aquarium, P.O. Box 3232, Vancouver, B.C., Canada, pers. commun., April 1989).

## Contrast in life history strategy

Notwithstanding the close systematic relationship between *A. japonicus* and *T. trichodon*, there are many life history features unique to each species, particularly with respect to the reproductive styles as discussed earlier. The terms and duration of their early developmental stages are shown in Figure 4, revealing that the egg stage of *T. trichodon* is almost four times longer than that of *A. japonicus*; however, the time when the larvae of both species appear is restricted to the spring seasons. The mechanism of this synchronized hatching is unknown, but plausible advantages are apparent. It is obvious that spawning substrates play an important role in producing these contrasting patterns of development. Perhaps the specialized mode of egg deposition unique to *A. japonicus* has evolved in close association with the abundant substrates represented by *Sargassum* spp., whereas, as suggested Marliave (1981), most plant substrates would have been too transitory to act as an egg deposition site for *T. trichodon*.

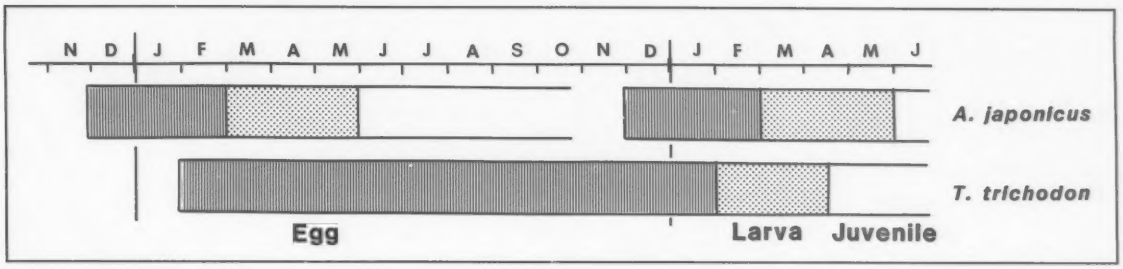


**Figure 4**
Comparison between terms and duration of early developmental stages of *Arctoscopus japonicus* and *Trichodon trichodon*. For sources, see text.

These ecological differences in spawning are compared with seasonal variations of the surface water temperatures among several stations covering most of the distribution areas of the two species (Fig. 5). By inspection, the location of two groups of stations may be recognized as corresponding to the zoogeography of the two species. Temperature ranges for *A. japonicus* are uniformly broader than those for *T. trichodon*: −2°-10°C to 18°-25°C versus 2°-7°C to 9°-14°C. Furthermore, temperature differences where the two species occur are particularly great during the warmer seasons. In the Sea of Japan, *A. japonicus* apparently copes with these extreme environmental conditions by precisely timing their early ontogeny to cold seasons and by gradually shifting the habitat toward deeper levels (up to 200–300 m) as growth proceeds (Nishimura 1969, Minami and Tanaka 1985).

Alternatively, the lowest temperature ranges of the eastern Pacific stations lie intermediate to those of the western Pacific stations. This stands in sharp contrast with the highest temperatures, which are not overlapping. Considering the year-round occurrence of the eggs of *T. trichodon* in the rocky intertidal area, it is quite natural to suppose that this species demands a particular set of physical environmental conditions for the specific spawning site, such as less variable water temperatures and above-freezing temperatures. These specific thermal conditions may also be responsible for the indistinct ontogenetic migration of *T. trichodon*.

Although there is no reliable information on the abundance of *T. trichodon*, except catch data of Allen and Smith (1988), *A. japonicus* surely has greater stocks than the former species. Total landings of *A. japonicus* in the Sea of Japan by Japanese vessels peaked at $3.3\times10^4$ tons in 1966. Of these, $2.1\times10^4$ tons were caught in the restricted area along the northwestern district of the Japanese mainland, namely, Akita Prefecture, where one of the biggest spawning grounds occurs regularly (Okiyama 1970, Kato 1980).

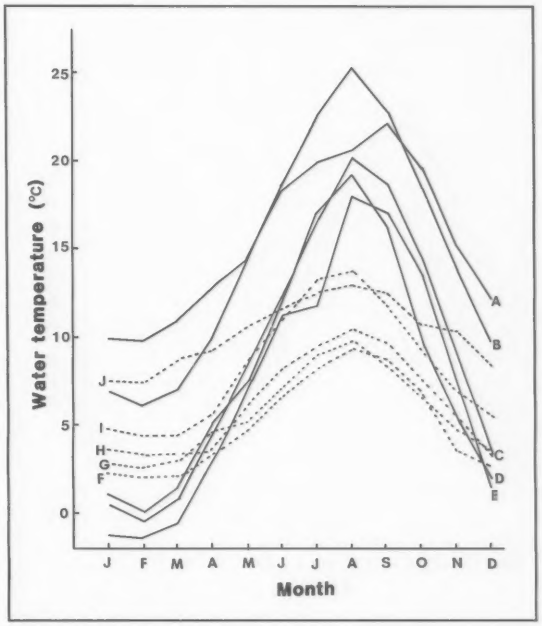


**Figure 5**
Seasonal patterns of surface-water temperatures from ten stations within the ranges of *Arctoscopus japonicus* (A–E, solid lines) and *Trichodon trichodon* (F–J, dotted lines) (adapted from Wadachi 1960). For locations, see Figure 1.

Figure 6 shows the long-term fluctuations of the catches of *A. japonicus* in this district. Coastal catches, comprised exclusively of fully matured specimens, are separated here from the total catches. Drastic changes in catches occurred during a 30-year period with peaks occurring around 1965–68 and 1974–75. The decrease between these peaks is slight as compared with the events in other periods such as around 1955 and after 1978. In 1984, the coastal catch dropped to a low of

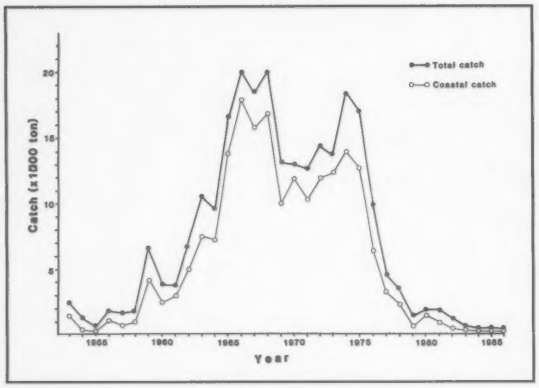


**Figure 6**
Fluctuation of the catch of *Arctoscopus japonicus* in Akita district, the northern Sea of Japan (after Ikehata 1987).

only $10^3$ tons from the maximum record of about 18 000 tons in 1966; the maximum/minimum ratio was about 180. Such drastic fluctuations may be extremely rare among demersal fishes, and a ratio of about 180 would be exceptionally great even among pelagic fish stocks (Funakoshi 1988). Usually these fluctuations are attributed to heavy fishing on a parent stock after the appearance of several poor year-classes, or conspicuous recruitment success in particular periods (Lasker 1981). It is alo generally accepted that success or failure in survival during the early period of ontogeny is critically important for successful year-classes.

In addition to the early-life-history traits, rearing experiments suggest that early larvae of *A. japonicus* have many adaptive features promoting survival. They include an early onset of exogenous feeding paired with a long period of mixed feeding (mixed endogenous and exogenous feeding) in larvae 3 days after hatching to early juveniles of about 20 mm SL (Maekawa 1985). Likewise, Marliave (1981) observed an early onset of first feeding in *T. trichodon*, at about 48 hours after hatching in an aquarium. Prolonged mixed feeding is also possible in this species. This may suggest that starvation is not usually the main cause of mortality in early stages. Concerning other mortality factors, such as predation during the early larval period, no reliable information is available for either species.

The importance of mixed feeding as a feature of a developing organism was stressed by Balon (1986). He suggested that the flexibility provided by a varying duration of mixed feeding can facilitate changes in the entire life history of the species. In view of the characteristic mixed-feeding feature of early stages of these two species, their contrasting ontogeny seems to be largely explained within this context. Possibly, slight differences in size and yolk volume in newly hatched larvae of the two species are responsible for creating the observed dichotomy in their life history patterns: *A. japonicus* developed the indirect type of ontogeny, having a distinct pelagic larval stage and demersal juveniles with intervening metamorphosis; *T. trichodon* developed the rather direct type of ontogeny having no distinct pelagic larval stage.

These contrasting life history patterns may be closely associated with the probable differences of their stock sizes. For example, the highly derived nature of ontogeny in *A. japonicus*, including the locally restricted spawning grounds, the specialized spawning method, the remarkably precise spawning season, and the typical sequence of early developments, may imply a high likelihood of a greater sensitivity of stock size to environmental changes. Of these features, the presence of so-called "first metamorphosis" (Youson 1988) should be emphasized because this phase, although less drastic than than the others, is expected to play a significant role in regulating successful transition events according to varying environmental situations.

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**Abstract.**—The sublethal effects induced by a model carcinogen and environmental contaminant on salmonid emergence behaviors have been studied. Rainbow trout embryos were exposed for 24 hours to 25 μg/mL of benzo[a]pyrene 1 week prior to hatching. Exposures occurred during the late organogenesis period of development and allowed assessment of how a single embryonic exposure might affect emergence behaviors nearly 6 weeks later. Though no differences in numbers of alevins successfully emerging were observed, a significant decrease was noted in performance of the upstream orientation behaviors characteristic of emergence among wild individuals. These findings are discussed in terms of a model describing the role of upstream swimming behavior after emergence.

# Decreased Performance of Rainbow Trout *Oncorhynchus mykiss* Emergence Behaviors Following Embryonic Exposure to Benzo[a]pyrene

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As aquatic ecosystems worldwide continue to function as ever-increasing reservoirs of environmental pollutants, the presence of many diverse classes of compounds is being documented (Champ and Park 1982). One class of compounds, the aromatic hydrocarbons, has been implicated in carcinogenesis in feral fish populations (Baumann 1989). Previous studies (Ostrander et al. 1988, 1989) and work presented here suggest that aromatic hydrocarbons may also exert subtle, yet profound, behavioral effects during early development.

Benzo[a]pyrene (B[a]P) is an aromatic hydrocarbon that is combustion product of organic materials (e.g., forest fires). Furthermore, anthropogenic activities have introduced significant amounts of B[a]P into the aquatic environment both directly (industrial emissions and oil spills) and indirectly (automobile exhaust and coal burning). This compound has been well studied in mammalian systems (reviewed in Gelboin 1980), and much is known of its mode of action. Recently we have verified the sensitivity of coho salmon early-life-history stages to a single embryonic exposure to benzo[a]pyrene (Ostrander et al. 1988). Embryonic exposure to B[a]P resulted in temporal differences in hatching, reduced and altered emergence success, and decreased foraging efficiency.

We next studied emergence behaviors following embryonic B[a]P exposure of the rainbow trout *Oncorhynchus mykiss*. We describe the effect of B[a]P exposure on the emergence success and upstream swimming behavior. A qualitative model, utilizing data from our rainbow trout and coho salmon studies, is proposed to explain the effects of toxicants on these early life behaviors.

## Materials and methods

### Experimental animals and exposures

Two replicates of a single experiment with rainbow trout were conducted with eggs obtained from the McCleary Trout Lodge, Tacoma, Washington.

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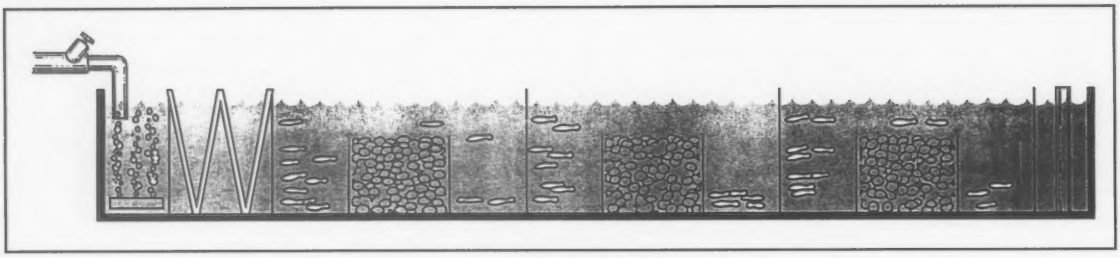

**Figure 1**

A single raceway containing three artificial gravel-filled redds and respective upstream and downstream compartments. Entering water was aerated and passed through a series of four baffles to reduce turbulence over the redds. Water exited through a standpipe at the opposite end of each raceway. Emerging fish, after entering either the upstream or downstream compartment, were removed and scored 3–5 times daily.

Eggs of a single female were fertilized with the pooled sperm of 12 males. Following fertilization, eggs were suspended in a continuous flow of lake water regulated with dechlorinated city water to a constant temperature of 12° ±1°C. One week prior to hatching (late organogenesis), eggs were divided into three groups of 150 eggs and each group was transferred to glass petri dishes for a 24-hour exposure in a volume of 0.4 mL water per egg. B[a]P (Aldrich Chemical Co, Product #B1,008-0) was suspended in spectrophotometric grade DMSO (Schwarz/Mann Biotech, Product #820636) to make a stock solution of 10 mg/mL. This solution was diluted in lake water to make the final exposure concentrations of 25 μg/mL. The control groups were exposed to filtered lake water, the solvent control group was treated with 0.5% solution of dimethylsulfoxide (DMSO) in filtered lake water, and the exposure group was treated with 25 μg/mL of B[a]P in 0.5% DMSO in lake water.

### Experimental apparatus

Artificial redds were constructed in replicate raceways by subdividing each raceway into ten compartments (Fig. 1). The upstream compartment contained baffles to reduce water turbulence in the redds. The remaining nine compartments included three redds (30 cm wide × 40 cm long) each occupying a single compartment and centered between an open upstream and downstream compartment (30 cm wide × 20 cm long). The redds consisted of smooth rocks (2–4 cm diameter) contained within perforated stainless steel plates. Adjacent open compartments were separated by plastic netting. The redd surface was within 8 cm of the water surface and the open compartments were 20 cm deep. The water, filtered to remove large particulates, flowed through each raceway at a velocity of 45 cm/second.

Following exposure, the eggs were rinsed with lake water and buried 8–10 cm deep in artificial redds. The position of the various groups in each raceway was randomized. The redds were maintained in darkness throughout embryonic development at a temperature of 12.0° ±1°C. Beginning 60 days postspawning, the raceways were checked daily for emerged fry, and, following emergence of the first fry, the raceways were checked three to five times daily. Alevins emerged and held station above the redds while orienting against the water flow. After several minutes they would (1) swim into the upstream compartment, (2) swim into the downstream compartment, or (3) drift backward into the downstream compartment.

### Data collection

The presence of an alevin in either the upstream or downstream compartment provided a quantitative measure of the ability of the fish to perform its typical upstream swimming behavior. Fish in the upstream and downstream compartments were counted and removed. Furthermore, 20 fry from the upstream and downstream compartments of each exposure group were randomly selected for measurements of total length, dorsal fin height, caudal fin height, pectoral fin height, anal fin height, and dry weight. An analysis of variance followed by a Student-Newman-Kuels multiple range test was used to test for significant differences among the means of the various exposure groups.

## Results

Rainbow trout were exposed to a sublethal 24-hour pulse (25 μg/mL) of B[a]P during late organogenesis. The emergence success of rainbow trout treated with

Mention of trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

**Table 1**

Emergence and upstream swimming behavior of rainbow trout and coho salmon, showing number of fish performing each behavior. In each experiment 150 apparently healthy salmon or trout eggs (embryos) were buried 1 week prior to hatching.

| Replicate number | Fish species | Exposure group | Number emerged | Number upstream (% of emerged) | Number downstream |
|---|---|---|---|---|---|
| 1 | Rainbow trout | Control | 136 | 103 (76) | 33 |
| | | DMSO | 138 | 104 (75) | 34 |
| | | B[a]P | 147 | 68* (46) | 79 |
| 2 | Rainbow trout | Control | 139 | 115 (83) | 24 |
| | | DMSO | 145 | 115 (79) | 30 |
| | | B[a]P | 143 | 60* (42) | 83 |
| 3[a] | Coho salmon | Control | 148 | 132 (89) | 16 |
| | | DMSO | 142 | 115* (81) | 27 |
| | | B[a]P | 118** | 76** (64) | 42 |
| 4[a] | Coho salmon | Control | 147 | 137 (93) | 10 |
| | | DMSO | 150 | 105* (72) | 45 |
| | | B[a]P | 103** | 70** (68) | 33 |

[a]Data from Ostrander et al. 1988.
*Significantly different from control group at $P<0.05$, chi-square analysis.
**Significantly different from control group at $P<0.001$, chi-square analysis.

**Table 2**

Morphological development of rainbow trout alevins at emergence. Values are means and ranges for groups of 20 fish.

| Group | Total length (mm) | Dry body weight (mg) | Caudal fin height (mm) | Dorsal fin height (mm) | Pectoral fin height (mm) | Anal fin height (mm) |
|---|---|---|---|---|---|---|
| Upstream control | 24.29 (22.6–25.6) | 44.09 (43.9–44.4) | 4.53 (3.8–5.0) | 1.86 (1.5–2.2) | 2.52 (2.2–3.2) | 1.67 (1.4–2.0) |
| Downstream control | 24.13 (21.5–25.1) | 44.61 (44.4–44.9) | 4.85 (4.0–5.6) | 1.86 (0.8–2.3) | 2.85 (1.9–3.3) | 1.80 (0.8–2.1) |
| Upstream DMSO | 24.41 (23.1–25.2) | 44.47 (44.2–45.1) | 4.69 (3.9–5.2) | 1.80 (1.5–2.3) | 2.96 (2.6–3.3) | 1.80 (1.5–2.1) |
| Downstream DMSO | 24.02 (21.4–24.9) | 44.52 (44.3–44.8) | 4.91 (4.3–5.4) | 1.90 (1.4–2.3) | 2.87 (1.8–3.3) | 1.79 (1.4–2.1) |
| Upstream B[a]P | 24.19 (21.4–25.5) | 44.17 (43.9–44.5) | 4.53 (3.8–5.4) | 1.75 (0.8–2.1) | 2.59 (1.9–3.3) | 1.63 (1.4–2.3) |
| Downstream B[a]P | 24.17 (23.3–24.9) | 44.33 (44.1–44.6) | 4.56 (4.0–5.2) | 1.96 (1.6–2.4) | 2.63 (2.3–3.0) | 1.77 (1.4–2.1) |

B[a]P was not significantly different ($\chi^2$, $P<0.05$) from embryos treated with DMSO (solvent controls) or filtered lake water controls (Table 1). In both replicates more than 95% of B[a]P-exposed fish successfully emerged.

The two B[a]P-exposed groups, however, exhibited a decreased tendency to orient upstream when compared with DMSO or untreated controls ($\chi^2$, $P<0.001$). Normal upstream orientation observed among emerged untreated and DMSO solvent controls was 75–83% of emerging alevins, while among B[a]P-treated groups less than 46% of the emerged alevins reached the upstream compartment (Table 1).

Measurements of total body length, dry weight, and caudal, dorsal, pectoral, and anal fin heights are summarized in Table 2. There were no significant differences in the morphology of upstream and downstream fish or between respective groups when tested with a one-way analysis of variance.

## Discussion

The salient result of these studies is that both rainbow trout and coho salmon exposed as embryos to a sublethal dose of B[a]P exhibit decreased ability to swim upstream after emergence from artificial redds.

Emergence and orientation are activities that terminate a sequence of early-life behaviors critical for salmonid survival. Following hatching, developing salmonid eleutheroembryos remain in gravel redds for 2–4 months until yolksac absorption and fin development are nearly complete (Fast 1987). As yolksac reserves are exhausted the eleutheroembryos migrate, primarily at night, to the upper layers of the redd. Emergence is complete when eleutheroembryos, now called fry, leave the redd and swim to the water surface to inflate the air bladder and begin feeding. The direction in which emergent fry migrate is species-specific. Coho salmon and rainbow trout fry typically orient and swim upstream to counteract downstream transport and to colonize natal and nearby streams unavailable to, or not used by, spawners (Mason 1976). Soon after emergence, fry establish and defend territories as feeding begins (Chapman 1962, Mason and Chapman 1965).

Our previous work (Ostrander et al. 1989) demonstrated that the lipophilic nature of B[a]P coupled with the expansive yolksac reserves of the embryo resulted in significant uptake of the compound and, furthermore, the B[a]P was only gradually lost from the egg throughout development. We found that over 60% of the B[a]P is retained in the eleutheroembryo at hatching when this exposure regimen is utilized. Consequently, rather than exposing our B[a]P-treated fish to an acute 24-hour pulse of B[a]P, they faced continuous exposure to B[a]P and its harmful metabolites (Gelboin 1980) as they exhausted their yolk reserves throughout early development.

There were no significant differences in numbers of fish emerging among the various control and exposure groups. Yet, fewer rainbow trout exposed to B[a]P as embryos exhibited typical upstream swimming behavior following emergence. These results are similar to previous findings for coho salmon (Ostrander et al. 1988). In that study, however, significantly fewer coho salmon, successfully emerged (Table 1). Perhaps the larger size of the coho alevin coupled with compromised abilities due to B[a]P exposure resulted in reduced success in negotiating the intersticial spaces of the redd during emergence. Fish in the downstream compartment did generally appear less active than fish in the upstream compartment. In neither study, however, were significant differences in weight or fin development among control and treatment groups observed, nor were any morphometric differences detected between fish going upstream or downstream in the experiments.

In these experiments, fish emerged from the gravel and oriented into the water flow. After about 1 minute, the majority of fish moved into the upstream compartment of the test apparatus. A smaller number of fish, generally less active, either swam or drifted into the downstream compartment. Successful upstream movement requires that the time to travel the distance across the redds is less than the time to become fatigued, assuming that fish in the downstream compartment became fatigued before they reached the upstream compartment. This is expressed, $T_f > T_t$, where $T_t$ is the travel time to the upstream compartment and $T_f$ is the fatigue time of the fish. Travel time to the upstream compartment depends on the average velocity of the current across the redds, $U$, the average fish swimming velocity, $V$, and the distance, $L$, it travels across the redd, and is expressed:

$$T_t = L/(V-U).$$

Fatigue time also depends on swimming velocity. Laboratory experiments indicate that among adult rainbow trout, the time to fatigue decreases exponentially with swimming velocity for velocities above 3 body lengths per second (bl/s). However, at 2 bl/s adult rainbow trout can swim indefinitely (Beamish 1978). Alevins probably have a similar relationship, although (due to smaller size) they can maintain considerably larger swimming velocities on a body length basis, exceeding 30 bl/s (100 cm/s) (Ostrander et al. 1989). The model assumes time to fatigue is infinite when swimming velocity is zero and decreases as swimming velocity increases. A simple power function has these properties:

$$T_f = k\, V^{-a}$$

where $k$ and $a$ are parameters that depend on condition of the environment and the fish. Equating the two time scales, a critical stream velocity is defined:

$$U^* = V - L/kV^a$$

where successful upstream migration requires $U < U^*$. The intersection of $U$ and $U^*$ defines a swimming velocity range required for successful movement into the upstream compartment (Fig. 2). For velocities outside the allowable range fish become fatigued before they reach the upstream compartment.

The experiments indicated that fish exposed to B[a]P had a greater chance of ending up in the downstream compartment. This result could be achieved if fish

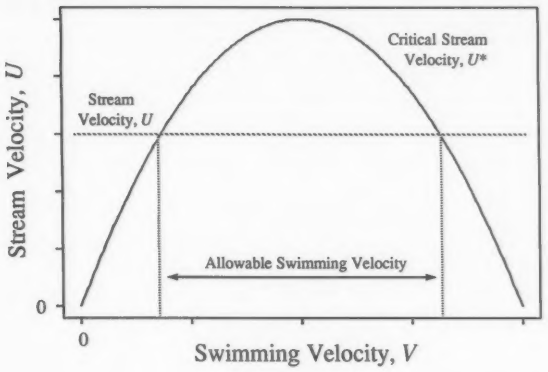


**Figure 2**

Critical stream velocity curve. Successful upstream movement requires that the critical stream velocity is greater than the stream velocity. Intersection of $U$ and $U^*$ defines the allowable swimming velocity, $V$, required for successful movement into the upstream compartment.

exposed to B[a]P became fatigued faster or swam upstream slower. In the first case, the critical stream-velocity curve of exposed fish would fall below the curve for unexposed fish. In the second case, the lower swimming velocity of the exposed fish would fall outside the allowable velocity range for successful upstream migration. The experiments were not designed to resolve such differences.

The model provides a qualitative basis for interpreting the experiments. It differs from standard dose-response models that describe the degree of change as a continuous function of the level of duration of toxicant exposure (Krewski and Brown 1981). The model allows a possible interplay of behavior and stamina for successful upstream movement, although such a separation was not pursued in the study.

Our results indicate that low levels of toxicants may affect important early-life-history behaviors critical to survival. Though the concentration of B[a]P used in this study is not frequently encountered in nature, the value of this study in predicting what could happen following some type of major accidental spill or discharge should not be overlooked. Given that a single 24-hour pulse of B[a]P elicited significant behavioral changes, future studies could be directed at understanding the potential effects of low-level chronic exposures which may more accurately mimic natural conditions.

## Acknowledgments

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# Age and Growth of the Antarctic Fish *Nototheniops nudifrons**

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**Abstract.**–Sagittal otoliths of the Antarctic fish *Nototheniops nudifrons* (Family Nototheniidae) contain internal microincrements which are visible by scanning electron microscopy. Microincrements were deposited on a daily basis, as validated through tetracycline and acetazolamide marking experiments. This was the first validation of daily microincrement deposition for any Antarctic fish. Daily formation of microincrements continued throughout the year, including during the winter when daylight periods were short. Counts of daily microincrements in the otoliths of 32 juveniles and adults allowed the determination of age and growth rates. From this sample, a multivariate regression model relating fish age to otolith morphometrics and fish size demonstrated that age could be estimated reliably from sagittal otolith weight and length. Age was estimated for a large sample of *N. nudifrons*, which allowed the determination of growth and natural mortality. Fish grew slowly (15 mm per year), reaching sexual maturity at an age of 4–5 years, with the largest fish attaining ages of more than 8 years. Growth and survivorship were similar for males and females.

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The Antarctic fishes are characterized by a high degree of endemism and extensive adaptations to their unique environment (DeWitt 1971). Although commercial exploitation of several species has begun, much of their basic biology is still poorly understood (Kock et al. 1985). Of special importance to ecological and fisheries research is determination of the age of fish captured in the field. Growth, mortality, and fecundity can be derived from age data. Ageing studies can also provide basic life-history information, such as population structure, and changes in population growth due to environmental perturbations. These age-related data increase our understanding of fish biology and form the basis of population dynamics models.

Antarctic fishes appear to be slow growing and long lived (Shust and Pinskaya 1978, Freytag 1980a, Kock et al. 1985, Radtke et al. 1989). Although age and growth of Antarctic fishes have primarily been determined by counting scale annuli (Olsen 1954, 1955; Wohlschlag 1961, 1962; Everson 1970, 1980; Shust and Pinskaya 1978; and others), the results from this technique are often difficult to interpret and especially unreliable for older fishes, as scales may be regenerated or resorbed (Mugiya and Watabe 1977; Freytag 1980a, 1980b). Therefore, an alternative ageing method, such as otolith increment analysis, is desirable. In contrast to scales, otoliths are neither regenerated nor resorbed, and are the most precise structure for ageing of fishes (Six and Horton 1977, Campana and Neilson 1985).

Otoliths are calcium carbonate structures deposited in the membranous labyrinth of the inner ear of fish. The otoliths of many fishes grow by daily accretion of layered increments (Pannella 1971). These increments are visible in sectioned otoliths as concentric rings, which can be enumerated to provide estimates of the age of temperate and tropical fishes (Pannella 1971, 1974; Campana and Neilson 1985; Jones 1986). Otoliths of temperate fishes may also form annual increments or annuli.

Several studies have utilized otoliths to age Antarctic fishes. Olsen (1955) found that the otoliths of icefishes were small and difficult to analyze by light microscopy. Rings in the otoliths of the icefishes *Chaenocephalus aceratus* and *Champsocephalus gunnari* were interpreted to be annuli (Olsen 1955). Subsequently, other researchers used rhythmic patterns in Antarctic fish otoliths for age determinations (Hureau 1966, Everson 1980, Freytag 1980b, North et al. 1980, Mucha 1980, Chojnacki and Palczewski 1981, Kock 1981,

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Sosinski 1981, Kochkin 1982, Burchett et al. 1984). These patterns were interpreted to be annuli; however, no validation data were available for the deposition rates of these increments. These presumed annuli, which are often difficult to discern and interpret, may not represent yearly growth increments (Scherbich 1975, Freytag 1980b, Radtke and Targett 1984).

Townsend (1980) described the presence of microstructural growth increments in Antarctic fish otoliths. These increments appeared to be analogous to the daily increments found in a host of fish species (see review by Campana and Neilson 1985). Such microincrements were used by Radtke and Targett (1984) to age *Notothenia larseni*, and are the foundation for the present research. However, the daily or annual nature of rhythmic patterns in otoliths has not been experimentally validated for any Antarctic fish species. Microincrements may generally form in response to changes in daily periods of light and dark (Radtke 1984), suggesting that special problems may exist in the formation of daily increments during times of short daylight in the winter months.

Management programs for Antarctic fisheries require knowledge of population parameters of both commercial and sympatric, non-commercial, species. *Notothenios nudifrons* (=*Notothenia nudifrons*) is among the most abundant demersal fishes in many habitats of the Antarctic Peninsula (DeWitt 1971). As such, this species may play a major role in the trophic structure of the Antarctic marine community, both as competitor with and prey for commercial species.

We recently reported on the reproductive biology of *N. nudifrons* (Hourigan and Radtke 1989). In the present study, the age and growth of *N. nudifrons* were determined by the examination of microincrements in sagittal otoliths. Microincrement deposition rates during different seasons were tested under experimental conditions. Correlations of age to otolith morphometrics allowed ageing of a large sample of fish and an estimation of their natural mortality rates.

## Methods

### Collection of fish and initial measurements

A total of 32 *Notothenios nudifrons* were collected on 28 March and 17 April 1985 by otter trawl in 54–110 m depths off Low Island (63°24′S to 63°27′S; 62°07′W to 62°17′W). An additional 30 fish were collected in the same area in February 1984, and used for preliminary otolith validation studies. All individuals were transported live to Palmer Station and placed in tanks with flow-through seawater. In addition to these fish, scuba divers collected three small juveniles near Palmer Station in Arthur Harbor (64°46′S; 64°04′W) in May and July 1985.

The fish from the 1985 trawls were analyzed for length-weight relationships and growth. Standard length (SL) and total length (TL) were measured to the nearest millimeter. Whole body weights were measured to the nearest 0.001 g. Otoliths were removed from all fish, cleaned, dried at 60°C, and stored in a desiccator. The gonads were examined to determine sex and reproductive condition (Hourigan and Radtke 1989).

The remaining fish were injected intramuscularly with acetazolamide (samples from 1985 only) or tetracycline (samples from 1984 and 1985) and kept in 500-L tanks with flow-through seawater, at ambient temperatures and natural photoperiods. Ten fish were kept in each tank, along with 10 *Notothenia gibberifrons*. Rocks were added to the tanks to provide shelter and nesting sites. Fish in tanks were fed *ad libitum* with krill every 2 days.

Fish were kept alive for a maximum of 158 days after injection, from April to October, at which time they were sacrificed, weighed, and measured. Otoliths of these fish were removed, cleaned, and stored dry in vials.

### Otolith structure and age determination from otolith microincrements

To determine the relationship of age to otolith size and shape, the length, width, and weight of sagittal otoliths were measured. Otoliths were segregated according to their lateral position in the cranium. Left and right sagittae from all fish were scanned using a computer-aided video digitizer, which produced a measure of maximum length (from the rostrum to antirostrum; nomenclature of Hecht 1978) and width (the widest distance in the dorsal-ventral plane). Otoliths were weighed on a microbalance to the nearest 0.01 mg.

A sample of 32 fish (from fish collected in 1985) was chosen for age determinations. This sample was composed of males and females of a representative size distribution. Left sagittae from these fish were attached to scanning electron microscope (SEM) viewing stubs with epoxy, carefully ground down to the central area by hand using a fine sharpening stone, and then polished with 0.3-micron alumina paste. The polished surfaces were etched for 1–20 minutes with 6% ethylene diamine tetraacetate (EDTA) with pH adjusted to 8 with NaOH. After etching, the sections were gently washed with water, dried, coated with gold, and viewed by SEM at various magnifications (50–10 000×).

Otoliths were examined for microincrements. A microincrement was defined as an unbroken incremental zone with discontinuous zones as boundaries (Radtke and Dean 1982). Sequential etching made it

feasible to enumerate all increments. Individual sections were etched for different lengths of time, with 15–20 minute etching times showing the inner increments most clearly, and shorter etching periods revealing the outer increments. Landmark scratches were placed on each section with an insect needle to follow increments uncovered by different etching times. The otolith was etched in steps of 1 minute and viewed with the SEM after each etching to follow the progression of the smallest increments found. Examination of the three-dimensional microstructure of the left sagitta demonstrated that the midtransverse plane was the best plane for routine sectioning.

### Validation of otolith ageing technique

Microincrements are generally assumed to be deposited daily (Pannella 1971, 1974; Radtke and Dean 1982; Radtke and Targett 1984). To test this, individual fish were given a single intramuscular injection of either tetracycline hydrochloride or acetazolamide at 0.025 mg/g body weight. Tetracycline is incorporated into the otolith and, viewed under a compound microscope with filtered reflected wavelengths of 700–800 nanometers, appears as a fluorescent band inside the otolith. Tetracycline marks are not visible by SEM. Acetazolamide is a carbonic anhydrase inhibitor which temporarily inhibits the calcification processes in the otolith resulting in a disruption band which can serve as a reference location for SEM study (Mugiya and Muramatsu 1982, Radtke unpubl. data).

Left sagittae from the fish injected with tetracycline were embedded in epoxy-casing resin and serially sectioned using a low-speed saw. The sections were polished as above, placed in nonfluorescent immersion oil, and examined under reflected ultraviolet light through a compound microscope. Otoliths with acetazolamide marks were prepared for SEM analysis as described above. The number of microincrements from the reference mark to the margin of the otolith was compared with the number of days between injection and the day that the fish was sacrificed.

### Relationship of otolith dimensions and fish age

In an effort to determine other predictors of age in *N. nudifrons*, the data generated from otolith and fish measurements were applied to the multiple regression model:

$$\text{Age} = a + b_1x_1 + b_2x_2 + b_3x_3 + b_ix_i$$

In this model, age in years was determined by counting microincrements, $a$ = intercept, $b$ = regression coefficients, $x$ = variables. The data were checked for normality, and the multiple regressions were determined in a stepwise fashion with the inclusion level for variables set at $p = 0.05$. As a measure of the variance associated with the otolith morphometric procedure, the percent of the total variance component due to variance between age estimates from the left and right sagittae of the same fish was calculated. Less than 5% of the total variance was due to variance between sagittae of the same fish (Table 1).

**Table 1**
Variance component due to within-fish variance in ages of *Nototheniops nudifrons* predicted from left and right otolith measurements, compared with variance among fish.

| Variance source | df | Sums of squares | Mean component | Variance | Percent |
|---|---|---|---|---|---|
| Between fish | 200 | 341.24 | 1.71 | 0.96 | 95.87 |
| Within fish | 200 | 6.08 | 0.04 | 0.04 | 4.13 |
| Total | 400 | 347.32 | 1.00 | 1.00 | 100.00 |

## Results

A total of 216 *Nototheniops nudifrons* were collected in trawls off Low Island. Five were caught during six deep trawls in 100–110 m depth, with the remaining fish caught in four shallow trawls at depths of 54–80 m. Fish captured in trawls ranged in size from 70 to 149 mm SL. More females ($N = 127$) were collected than males ($N = 74$), and the modal size of females (100 mm SL) was slightly larger than that of males (90 mm SL; Fig. 1). Three smaller juveniles (each 45 mm SL) were collected by hand in 10 m depth at Arthur Harbor.

### Length-weight relationships

Length-weight relationships of males and females are shown in Figure 2. Separate regression equations were calculated for males and females using a gonad-free body weight. Weight was approximately a cubic function of length, indicating nearly isometric growth. The length-weight relationship of the fish conformed to the power curve model Weight = $a(\text{SL})^b$. An analysis of covariance indicated that the slopes of the length-weight relationships for the sexes were not significantly different (df = 1, 203; $F = 2.30$, $0.05 < p < 0.25$). The conversion of standard length (SL in mm) to total length (TL in mm) was:

$$\text{TL} = 1.136(\text{SL}) + 1.529; (N = 216; R^2 = 0.99).$$

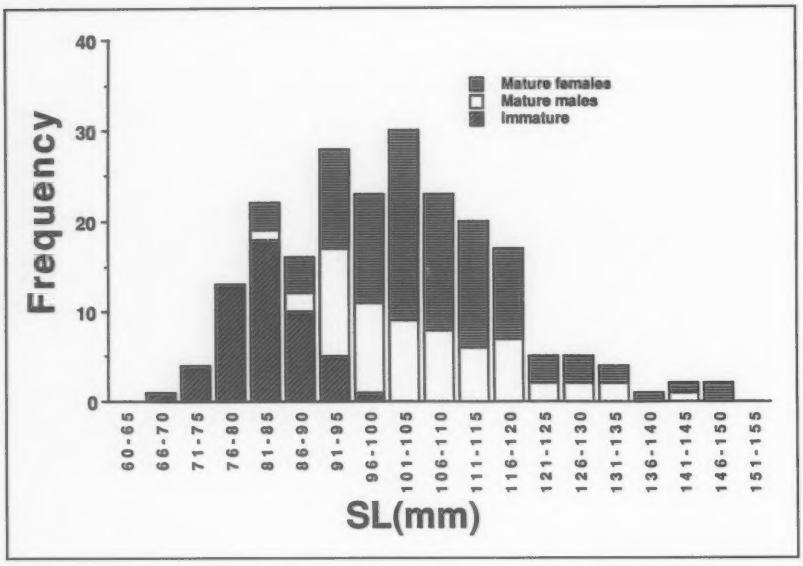



**Figure 1**
Length-frequency distribution of immature and sexually mature male and female *Nototheniops nudifrons* captured by trawls near Low Island in 1985.

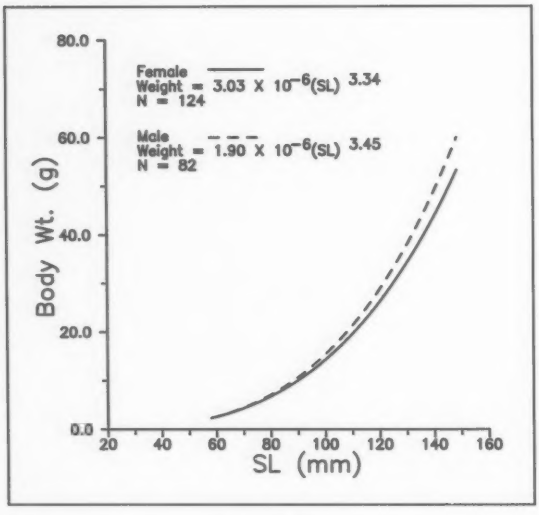



**Figure 2**
Length-weight relationship of male and female *Nototheniops nudifrons*. Wet body weight (with gonads removed) increased approximately as the cube of fish standard length (SL).

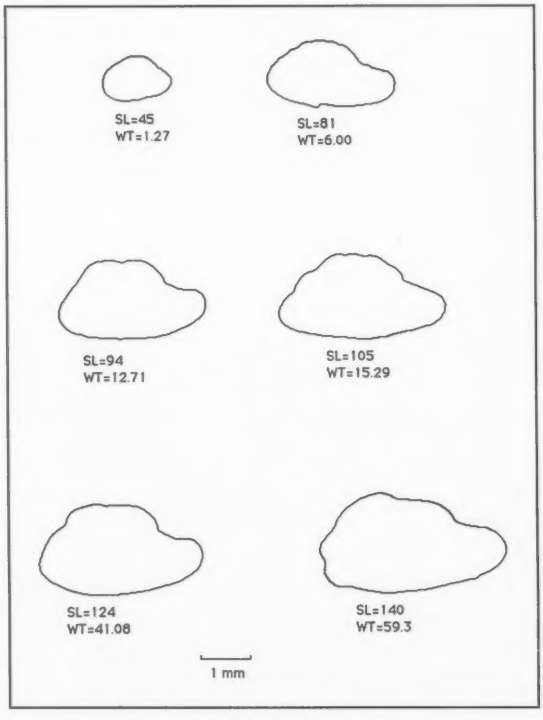



**Figure 3**
Change in size and shape of sagittal otoliths of *Nototheniops nudifrons* with increasing fish size. SL = standard length; WT = wet weight of fish.

## Description of otoliths

The sagittae of *N. nudifrons* were large and oval in shape (Fig. 3) with a well-defined rostrum. The size of the rostrum was directly proportional to fish size. The external surface was smooth and gently rounded. Sagitta length was related linearly to fish length (SL)

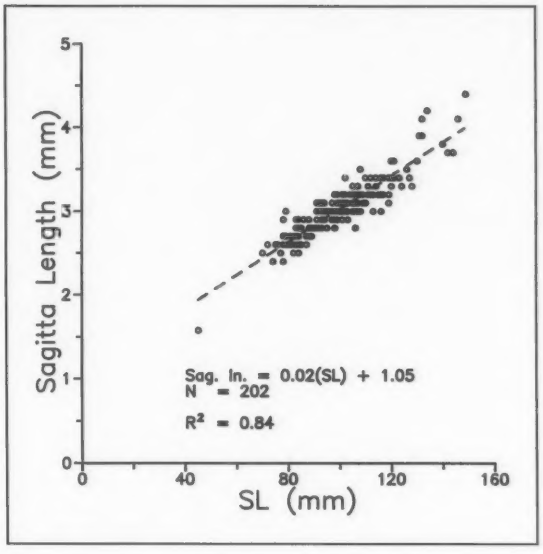



**Figure 4**
Relationship of sagittal otolith length to fish standard length (SL) for *Nototheniops nudifrons*.

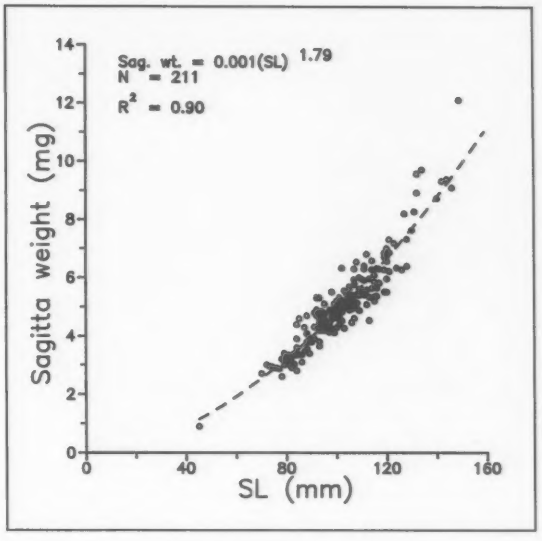



**Figure 5**
Relationship of sagittal otolith weight to fish standard length (SL) for *Nototheniops nudifrons*.

(Fig. 4), and sagitta weight was related exponentially to fish length (SL) (Fig. 5). Ground, polished, and decalcified sagittae were examined by SEM. A low magnification view of a sagittal otolith (Fig. 6) shows increments occurring concentrically from the center to the edge. Larger incremental patterns, or bands, were observed, but they could not be attributed to any specific environmental cues. Counts of microincrements within these bands showed that they were not true annuli. Sagittae exhibited a well-defined central core region or nucleus (Fig. 7a). Within the core region were concentric microincrements separated from the surrounding otolith by a distinct transition zone (Fig. 7b). Surrounding the core area were mineral crystals in a protein matrix which formed microincrements (Fig. 8a and 8b). Counts of microincrements were made beginning at the core transition zone and ending at the outer edge of the otolith. These microincrements varied in width from about 2 μm (Fig. 8a) to less than 1 μm (Fig. 8b). Differences in increment width may reflect periods of differential growth.

## Validation of the daily nature of microincrements

The periodicity of growth increment formation was examined using tetracycline- and acetazolamide-marked specimens which were held in tanks at ambient light and temperature regimes after injection. After injection of tetracycline or acetazolamide, *N. nudifrons* displayed some evidence of short-term stress, including cessation of feeding for 2 or 3 days, but only one mortality occurred. Subsequently, the fish survived well in captivity, with 80% of all fish surviving the whole winter. Sagittae of 29 fish injected with tetracycline in February and March 1984 and held 4–34 days under natural daylight photoperiods were examined for post-treatment increments. A discrete fluorescent band was discernible in all specimens, and increments between the band and the margin of the otolith were counted (Table 2). The number of increments averaged 2.5 increments less than the number of days after injection. This difference corresponded well to the initial period of stress, and did not change with length of the experiment (Median test, $0.2>p>0.1$; Siegel 1956). Linear regression analysis (Model I, Sokal and Rohlf 1969) indicated that the slope ($b = 1.076$, 95% CI of 0.756–1.396) was not significantly different from 1 (Table 2). The $y$-intercept equaled −3.27 (95% CI of −7.73–1.19).

Sagittae from five fish injected with acetazolamide in April 1985 were examined by SEM. A discrete disruption of increments caused by the interruption of calcium deposition was discernible (Fig. 9). The number of increments from this disruption mark to the otolith margin averaged 9.2 increments less than the number of days after injection (Table 2). Acetazolamide disrupts metabolic processes and its effects can be expected to last longer than the tetracycline's, since the latter does

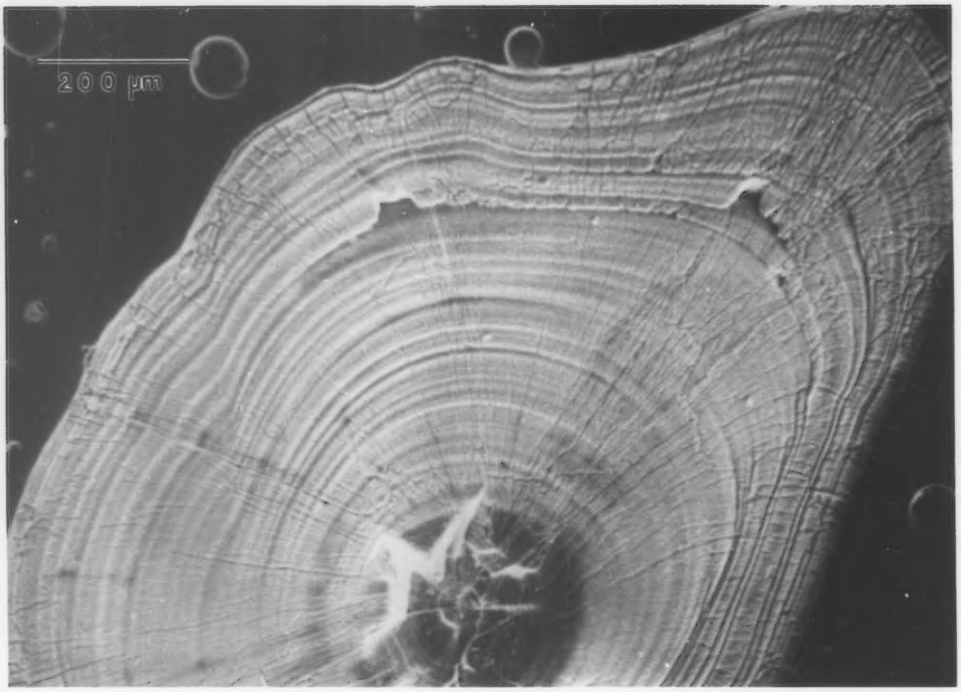



**Figure 6**
Low-magnification scanning electron micrograph of a sagittal otolith of *Nototheniops nudifrons*, showing concentric incremental patterns. The sagitta is from a 100-mmSL specimen.

not appear to affect the fish's metabolism. Linear regression results indicated a slope of 0.962 (95% CI of 0.983–0.941) and a $y$-intercept of −5.40 (95% CI of −2.80 to −8.01). The significance of this analysis is suspect because of the small sample size ($N = 5$). The discrepancy between postinjection days and microincrements counted increased from 5 to 12 with length of incubation period. However, this apparent increase in the discrepancy represents an actual percentage decrease in error from 50% to less than 10%. The longest incubation period in the acetazolamide experiment was 158 days, which was three times longer than the longest tetracycline incubation. This may explain why in the tetracycline experiment we did not observe an increase in the discrepancy between number of increments and days after injection.

During the experiment, the photoperiod varied from 9:15 hours Light:Dark, to a minimum of 5:19 L:D in June, to 15:9 L:D in October. The microincrements formed during incubation were uniform. Despite considerable variation in photoperiod, we found no indication that microincrements cease to form on a daily basis.

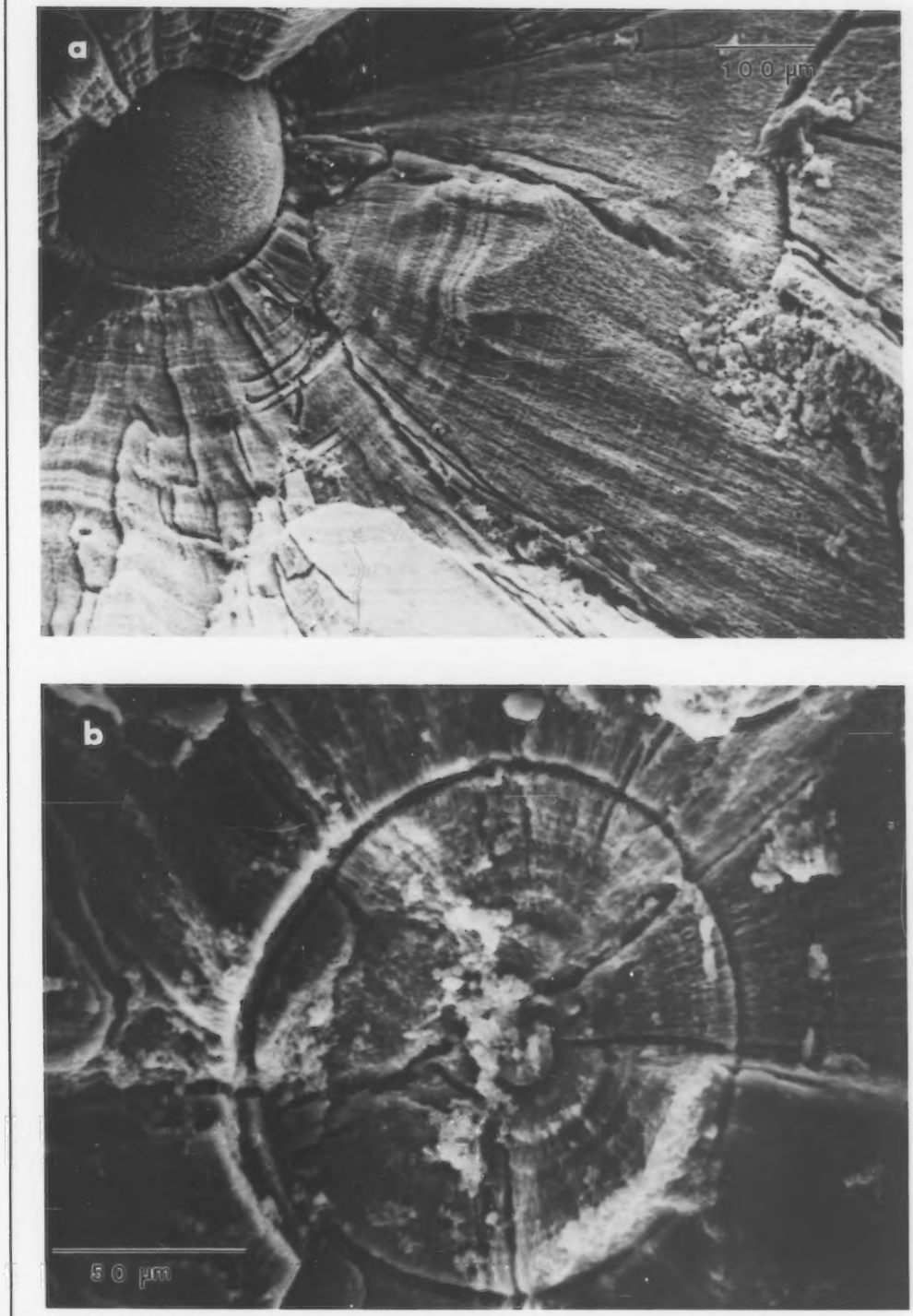
## Age and growth

Microincrements were counted in the sagittal otoliths of 32 fishes. Ages ranged from 1.3 years for the small juveniles collected by hand, to 8.5 years for the largest individual collected. Fish length was related to the number of microincrements in the sagitta (Fig. 10). Length (mm) increased linearly with age (years), and was best described by the equation:

$$SL = 14.87(\text{Age}) + 23.56; (R^2 = 0.93, p<0.0001)$$

No difference in growth was observed between the sexes in our sample (Fig. 10). When separate regressions were calculated for males ($N = 11$) and females

**Figure 7**
(a) Scanning electron micrograph of a sagittal otolith of a 130-mmSL *Nototheniops nudifrons*, showing the characteristic central core area, or nucleus, separated by a well-defined transitional zone from the outer zone with microincrements radiating outward. (b) Microincrements from a 100-mmSL fish found within the core area of the otolith.


a
100 µm
b
50 µm

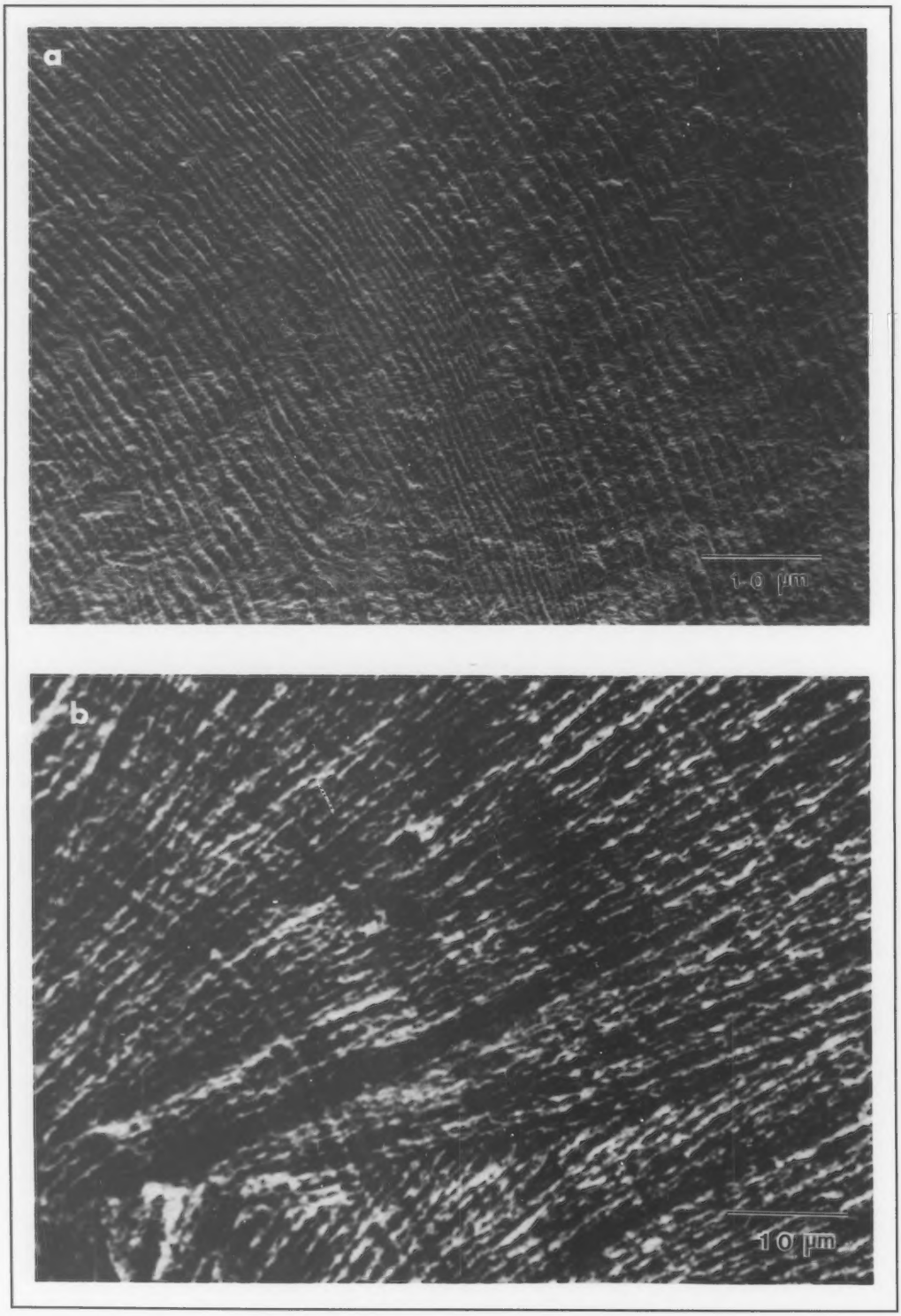

a
1.0 µm
b
10 µm

**Figure 8**

Scanning electron micrographs of microincrements of sagittal otoliths of *Nototheniops nudifrons*, as utilized for daily increment enumeration. (a) Wide and narrow patterns of microincrements from a 144-mmSL fish. (b) Narrow microincrements from a 70-mmSL fish.

($N = 18$), analysis of covariance indicated that the slopes of the two lines did not differ between the sexes (df = 1, 26; $F = 0.82$, $p > 0.37$).

## Relationship of fish size and otolith dimensions to fish age

Stepwise multiple regression analysis relating fish size (mm), weight (mg), and otolith morphometrics (sagitta length in mm and weight in μg) to age (years), resulted in the acceptance of the following model:

$$\text{Age (Yrs)} = 3.892 + 0.856(\text{sagitta wt}) - 2.206(\text{sagitta length}) + 0.041(\text{SL}) - 0.025(\text{fish wt})$$

Addition of the remaining variable (sagitta width) did not improve the regression ($N = 32$, $R^2 = 0.967$, $p < 0.05$; Table 3). The residuals were randomly distributed, which demonstrated that this multiple regression best explained the variability in age. Over 94% of the variance was explained by the regression of the two otolith measurements (weight and length). The variables in the model, such as otolith length, width, and weight, are not strictly independent variables, nor are length and body weight. This deviation from the assumptions of the model may result in an artificially inflated $R^2$ value; however, this should not decrease their practical value as predictors. Sagitta weight alone accounted for 92% of the variance in the regression, supporting the usefulness of otoliths as age-related structures.

The relationship between age and otolith morphometrics allowed the estimation of age for all the fish in the sample (Fig. 11). The growth curve derived from the multivariate model (Fig. 11) was comparable to that derived from microincrement counts (Fig. 10), and both were linear in form. Individuals in this population of *N. nudifrons* grow at approximately 15 mm per year, which is a slow growth rate. Analysis of covariance of

**Table 2**

Validation of the daily nature of otolith microincrement deposition in *Nototheniops nudifrons*. Otoliths of fish injected with tetracycline were examined by light microscope, while those injected with acetazolamide were examined by scanning electron microscope.

| Injection | Number of replicates | Days after injection | Number of post-treatment microincrements counted |
|---|---|---|---|
| Tetracycline | 1 | 4 | 1 |
| Tetracycline | 5 | 5 | 2,3,3,3,3 |
| Tetracycline | 2 | 6 | 3,3 |
| Tetracycline | 3 | 7 | 4,4,4 |
| Tetracycline | 2 | 9 | 5,7 |
| Acetazolamide | 1 | 9 | 4 |
| Tetracycline | 5 | 10 | 7,7,7,8,10 |
| Tetracycline | 1 | 11 | 6 |
| Tetracycline | 2 | 14 | 10,11 |
| Tetracycline | 2 | 15 | 12,12 |
| Tetracycline | 3 | 16 | 14,15,16 |
| Acetazolamide | 1 | 21 | 14 |
| Tetracycline | 1 | 24 | 23 |
| Tetracycline | 2 | 34 | 33,34 |
| Acetazolamide | 3 | 158 | 144,147,149 |

Regression analysis

| | Regression coefficient | SE | $t_S$ | df | $p$ |
|---|---|---|---|---|---|
| Tetracycline | $b$ = 1.076 | 0.074 | 1.027 | 27 | $0.4 > p > 0.2$ |
| | $y$-intercept = −3.268 | 1.036 | | | |
| Acetazolamide | $b$ = 0.962 | 0.0049 | 7.755 | 3 | $p < 0.01$ |
| | $y$-intercept = −5.402 | 0.606 | | | |

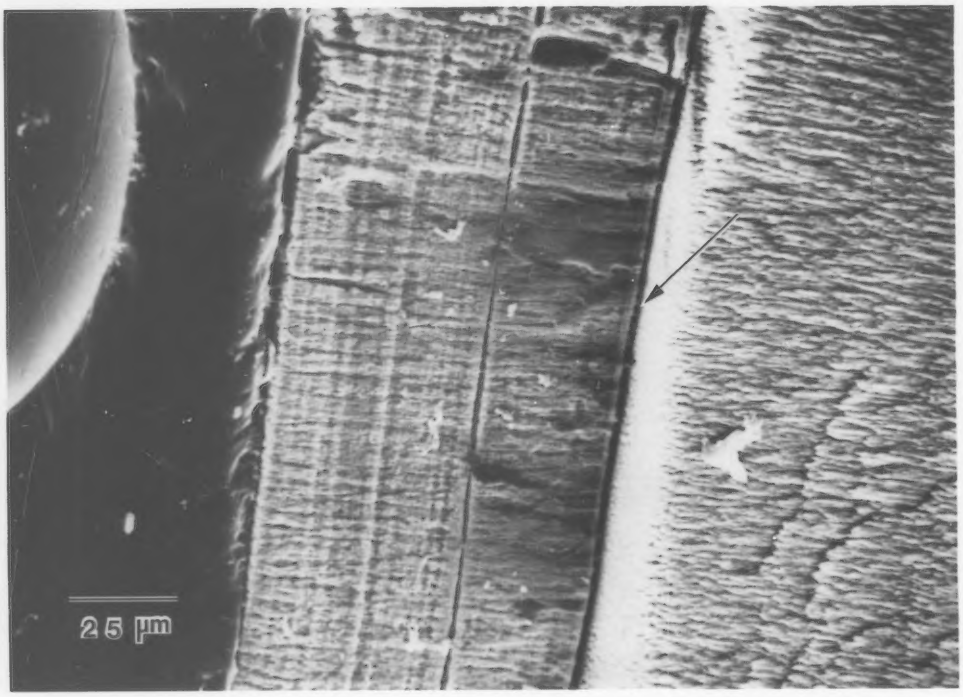



**Figure 9**
Scanning electron micrograph of a sagitta from a 100-mmSL *Nototheniops nudifrons* marked with acetazolamide. The acetazolamide mark (arrow) is visible as a disruption in the growth increments.

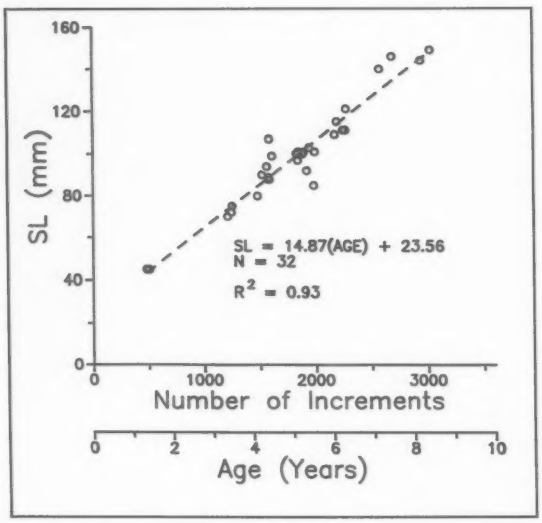



**Figure 10**
Regression of fish standard length (SL) on age as determined from the number of sagittal otolith microincrements for *Nototheniops nudifrons*.

**Table 3**
Associated statistics of one-way regression and stepwise multiple-regression model of fish age in years vs. size and weight variables for *Nototheniops nudifrons*. $N = 32$.

One-way regression

| Variable | $F$ | $P>F$ | Model $R^2$ |
|---|---|---|---|
| 1 Sagitta weight | 314.64 | 0.0001 | 0.921 |
| 2 Fish length (SL) | 213.31 | 0.0001 | 0.888 |
| 3 Fish weight | 134.64 | 0.0001 | 0.832 |
| 4 Sagitta length | 103.35 | 0.0001 | 0.793 |
| 5 Sagitta width | 92.43 | 0.0001 | 0.774 |

Multiple regression

| Step | Variable entered | $F$ | $P>F$ | Partial $R^2$ | Model $R^2$ |
|---|---|---|---|---|---|
| 1 | Sagitta weight | 53.68 | 0.0001 | 0.921 | 0.921 |
| 2 | Sagitta length | 23.16 | 0.0001 | 0.021 | 0.942 |
| 3 | Fish length (SL) | 17.43 | 0.0003 | 0.019 | 0.961 |
| 4 | Fish weight | 4.53 | 0.0437 | 0.006 | 0.967 |

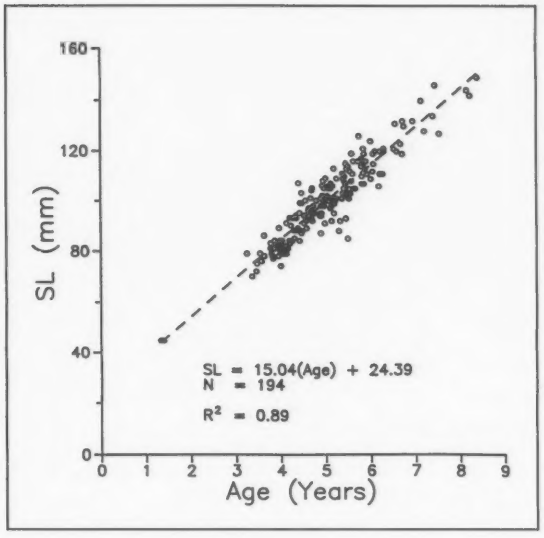



**Figure 11**
Regression of fish standard length (SL) on estimated age for *Nototheniops nudifrons*. Age was estimated by a multivariate mathematical model based on fish standard length, fish weight, otolith length, and otolith weight.

separate growth curves calculated for males and females showed no significant difference (df = 1,177; $F = 0.87$; $p > 0.36$), indicating that males and females grow at the same rate.

## Discussion

### Otolith microincrement deposition and age determination

The accuracy of age and growth estimates depends on the assumption that the microincrements viewed were deposited on a daily basis. Daily increments have been found in otoliths from many temperate and tropical fish species (see review by Campana and Neilson 1985). The daily nature of microincrement deposition in *Nototheniops nudifrons* was validated through the tetracycline and acetazolamide marking experiments. Daily increment deposition occurred even during the shortest days of the Antarctic winter. The formation of microincrements may become less regular in some fishes after sexual maturity (Pannella 1980), but our validation study included both immature subadults and mature males and females, which all deposited daily microincrements. Hourigan and Radtke (1989) found that daily microincrement deposition also occurs in larval *N. nudifrons*, beginning at or around the date of hatching. Together, these studies provide the first validation of daily otolith microincrements for any Antarctic fish.

In addition to the microincrements, the otoliths of *N. nudifrons* contained larger banding patterns. In temperate regions, environmental factors such as temperature and food availability show regular and marked seasonal changes, giving rise to clearly identifiable growth periods in fish otoliths. The regular annual formation of these seasonal rings in the otoliths of temperate fishes provides a successful and widely used ageing technique. Growth increments laid down in the otoliths of some Antarctic fishes may be annuli (e.g., *Harpagifer bispinis antarcticus*; Daniels 1983); however, those observed in this study, as well as those in the otoliths of *Nototheniops larseni* (Radtke and Targett 1984), are not. Nevertheless, such increments have been used, perhaps erroneously, for ageing purposes. Compared with temperate zones, Antarctic habitats undergo smaller fluctuations in temperature, which may result in a lack of distinct annual growth increments.

Daily microincrements allow the ageing of Antarctic species without otolith annuli. Microincrements are the result of a discontinuous zone which is generally formed under changing light conditions, probably at daybreak (Tanaka et al. 1981). The near-constant light and constant dark conditions experienced by Antarctic fishes during the summer and winter, respectively, could potentially interfere with daily deposition patterns. However, in the present study, daily increment formation continued despite great variation in photoperiod. Although areas in otoliths were detected in which increment width decreased (Fig. 8), none of these appeared to indicate a cessation of increment formation. Slight changes in light intensity, which occur in both Antarctic summer and winter, or endogenous rhythms may be responsible for the daily pattern of otolith deposition. This problem is currently being investigated using Antarctic fishes kept in constant dark or constant light, and under different light intensities (Radtke and Hourigan unpubl. data).

Use of a multivariate mathematical model relating age to otolith length and weight and fish size is a simpler method of age determination. The preparation and counting of microincrements in fish over 1 year of age is time-consuming and impractical. However, the multiple regression equation calculated from the 32 individuals analyzed with SEM provided an alternative ageing method. Otolith weight (with its consistent relationship to body length) was the best predictor of age, demonstrating the usefulness of otoliths in such a regression. This method should be applicable to other fish species, serving as a quick means to provide growth information. The dimensions of otoliths have been used to estimate the age of temperate fishes (Templeman

and Squires 1956, Boehlert 1985, Radtke et al. 1985). Otolith-age equations are species-specific and possibly population-specific. Using otolith morphometrics for ageing will, therefore, require developing the equations for individual species. Nevertheless, in conjunction with ageing techniques using microincrement counts, otolith morphometrics offer a simpler method of ageing a large sample of individuals than is possible using more laborious techniques.

The external features of *N. nudifrons* otoliths were distinctive compared with those from eight other Antarctic fishes examined (*Chaenocephalus aceratus, Champsocephalus gunnari, Harpagifer bispinis antarcticus, Notothenia angustifrons, N. gibberifrons, N. larseni, N. corriceps*, and *Trematomus newnesi*; Radtke, pers. observ.). Species-specific otolith features of Antarctic fishes have been described by Hecht (1987) and these may be useful in identifying Antarctic fishes from cetacean, pinniped, bird, or fish stomachs (Hecht 1987, North et al. 1984). Otolith morphological characteristics may also provide information on taxonomic relationships among Antarctic fishes (Hecht 1987), as they have for other fish groups (Hecht 1978, Hecht and Hecht 1978, Morrow 1979).

## Life history of *Notothenlops nudlfrons*

*Notothenlops nudifrons* is a slow-growing, relatively long-lived fish. Subadults and adults of both sexes were found in shallow-water (<100 m) benthic habitats along the Antarctic Peninsula, as reported by other researchers (Targett 1981, Daniels and Lipps 1978, Kellermann 1986). The absence of individuals smaller than 75 mm SL from trawls probably represented selection by the fishing gear for larger individuals. The growth curves determined by body length vs. microincrement count, as well as by body length vs. age calculated from the multivariate relations of otolith length and weight, were similar and linear in shape between 45 and 149 mm SL. Linear growth was observed even though the data included a large size-range of fish, with individuals near the largest sizes reported for this species. This type of linear growth, with no marked slowing toward an upper asymptote, has not been reported for other Antarctic fishes, although the growth curve of *Harpagifer bispinis antarcticus*, another small Antarctic fish, is nearly linear (Daniels 1983).

Males and females had similar growth rates. This was surprising, since mature males and females follow different strategies. Males and females reach sexual maturity at the same age (4–5 years); however, thereafter females invest much more energy into gonadal growth than do males (Hourigan and Radtke 1989). All parental care is provided by the males, which may spend at least 4 months in nest defense of a single clutch of eggs (Hourigan and Radtke 1989). This probably requires increased energy costs, and may limit food intake by constraining the male to foraging near the nest. These two strategies may entail similar energy expenditures, resulting in similar somatic growth rates.

Estimation of mortality rates is central to the determination of demographic parameters (Gulland 1955). It is possible to estimate natural mortality ($Z$) from the data on trawl catches and age for this population of *N. nudifrons*. The most widely used method to estimate mortality is the Beverton and Holt mortality estimator which uses the von Bertalanffy growth curve (Beverton and Holt 1956). The age-length data for the 32 fish were fitted to the von Bertalanffy growth curve, and the parameters and their confidence limits are given in Table 4. These values are primarily useful for comparative purposes, since the actual shape of the growth curve approximated a linear relationship. Natural mortality, calculated from the von Bertalanffy parameters and derived from the sample of 32 fish of known ages, yielded a value of $Z = 0.68$ (Table 4). When $Z$ was calculated using the von Bertalanffy growth parameters for the larger sample of 212 fish with predicted ages, $Z = 0.66$. These estimates assume that the fish grow according to a deterministic von Bertalanffy growth curve. Since the present sample was more accurately represented by a linear growth curve, this assumption was violated. An independent mortality rate was calculated using the actual age estimates from the otolith morphometrics. In this estimate, the mortality rate is the slope of the log-survivorship curve (Ricker 1975) and was calculated to be 0.89.

Kock et al. (1985) provide a summary of mortality estimates for larger Antarctic fishes of commercial interest. Both estimates of instantaneous mortality of *N. nudifrons* were higher than these estimates, which ranged from 0.20 to 0.35. Predation rates may be higher on *N. nudifrons* than on larger species. However, Daniels (1983) estimated the mortality of the still smaller *Harpagifer bispinis antarcticus* to be 0.22 and 0.25 for males and females, respectively (a recalculation of his data for both sexes combined, using the same methods as for *N. nudifrons*, resulted in a value of 0.223).

Although the high mortality rates for *N. nudifrons* accurately describe our sample, they may be subject to sampling errors. Our estimates were based on a single sample captured on two occasions 1 month apart. Both mortality calculations assume that the sampled population is age-stationary (i.e., the age distribution remains the same from year to year), an assumption which is frequently not met. Mortality estimates will also be biased if certain age classes larger than $L_C$ (length at first capture) are less subject to capture. Our

**Table 4**

Parameter estimates derived from the Von Bertalanffy growth equation ($L_\infty$ constrained to 160 mm SL), natural mortality rates, and associated parameters for *Nototheniops nudifrons* collected from the Antarctic Peninsula.

| | SL vs. age in days | | SL vs. age in years | |
|---|---|---|---|---|
| Parameter | Estimate | Confidence limits | Estimate | Confidence limits |
| | **From otoliths ($N = 32$)** | | | |
| $K$ | 0.0005 | 0.00049–0.00061 | 0.200 | 0.000–0.223 |
| $t_0$ | 2.20 | −158.10–162.50 | 0.006 | −0.434–0.445 |
| | **From predicted ages ($N = 194$)** | | | |
| $K$ | 0.00048 | 0.00047–0.00050 | 0.175 | 0.172–0.183 |
| $t_0$ | −40.848 | −94.681–12.986 | 0.112 | −0.259–0.036 |

| | **Mortality estimates (Beverton and Holt 1956)** | | |
|---|---|---|---|
| | All | Male | Female |
| $L_C$ | 101 | 91 | 101 |
| $L_{Mean}$ | 113.1 | 106.6 | 112.5 |
| $k$ | 0.175 | 0.175 | 0.175 |
| $Z$ | 0.678 | 0.599 | 0.73 |
| From estimated ages where the mortality rate $Z$ is the slope of the log-survivorship curve (Ricker 1975) | | | |
| $Z$ | 0.894 | 0.807 | 1.26 |

sampling caught significantly more females than males ($\chi^2$, $p<0.05$), and the modal size of males was smaller. This might mean that there are fewer large males in this population. Alternatively, larger males may be less subject to capture in spring, perhaps because of different habitat preferences of nesting males. This would skew mortality estimates upwards.

The life history of *N. nudifrons* is characterized by slow growth and a relatively long life for a small fish. Age at sexual maturity is late (4–5 years), and fecundity is low (Hourigan and Radtke 1989). Eggs take several months to hatch, followed by a pelagic larval stage of several months duration (Kellermann 1986, Hourigan and Radtke 1989). It has become clear that these life-history traits are the norm for Antarctic fishes (Daniels 1983, Kock et al. 1985). They combine to produce species that are vulnerable to overfishing and that recover slowly when stocks are depleted. Indeed, catches of both *Notothenia rossii* and *N. gibberifrons* on the shelves of certain islands of the Scotia Sea decreased drastically after several years of fishing (Kock et al. 1985). The methods used in the present study may provide more accurate estimates of the ages of Antarctic fishes, and facilitate management of Antarctic fisheries.

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# Distribution and Behavior of Queen Conch *Strombus gigas* Relative to Seagrass Standing Crop

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**Abstract.** – A study was conducted on shallow banks near Lee Stocking Island, Bahamas, to determine habitat associations of queen conch *Strombus gigas* L. within seagrass meadows of *Thalassia testudinum*. Transect data showed that conch density and biomass increased directly with increasing macrophyte cover up to an optimal level of moderate-density seagrass (608–864 shoots/m$^2$), after which conch density decreased sharply. Up to the optimal level, conch density and biomass were closely correlated with seagrass and detritus biomass, shoot density, and depth. Seagrass shoot density was the best predictor of conch abundance. Results of habitat choice experiments showed that two different juvenile size classes (75–100 mm and 125–150 mm shell length) are proficient in detecting and choosing habitats with moderate seagrass density over bare sand, low or high seagrass density. Larger conch appear to prefer habitat with higher shoot density than conch of smaller size classes; adult conch were less specialized in their habitat association. These results provide data on one of the key environmental variables, seagrass structure, which will be useful in predicting conch distributions in the field and for planning conch outplanting.

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Seagrass meadows, common in protected shallow waters, are known to be important sources of food and shelter for numerous fishes and invertebrates from high to low latitudes (Kikuchi 1980, Ogden 1980, Virnstein et al. 1984). Living seagrasses are consumed by a few animals such as surgeonfishes, halfbeaks, parrotfishes (Randall 1964, Ogden 1980), urchins (Lawrence 1975), green sea turtles (Ogden 1980), and sirenia (Bertram and Bertram 1968); however, most nonpredaceous fauna of seagrass meadows consume seagrass epiphytes or detritus (Zimmerman et al. 1979, Leber 1983, Fry 1984, Howard 1984, Kitting et al. 1984, Van Montfrans et al. 1984). Sheltering from predation has been shown experimentally for many seagrass inhabitants, particularly crustaceans (Nelson 1979, 1981; Heck and Thoman 1981; Coen et al. 1981; Stoner 1982; Leber 1985; Wilson et al. 1987).

The queen conch *Strombus gigas* L. is a large gastropod mollusc which derives both food and shelter from seagrass beds of the Caribbean region (Bermuda and southeastern Florida to Brazil). After the first year of life, of which little is known, queen conch juveniles emerge from the sediment and feed epibenthically in seagrass meadows where there are large quantities of algal and detrital foods (Randall 1964). Juvenile queen conch are important grazers of seagrass detritus, and conch densities may be limited by food abundance (Stoner 1989). Recent experiments conducted in the Bahamas have shown that seagrasses reduce predation rates on juvenile conch in nursery areas (Marshall and Lipcius, In review).

Throughout its geographic range, the queen conch is an important commercial species which has been severely depleted in many areas (Adams 1970, Brownell et al. 1977). For this reason, there is increasing interest in improving the management of conch, and seeding of depleted areas with hatchery-reared juveniles has been proposed (Berg 1976, Brownell and Stevely 1981, Laughlin and Weil 1983, Coulston et al. 1987). Successful management of the fishery and/or outplanted populations will require detailed information on the relationships between queen conch and environmental variables. This study was conducted to examine the role of macrophyte cover in the distribution of juvenile conch in two nursery areas of the Exuma Cays, Bahamas. In addition to seagrass shoot density and biomass, abundance of detritus, sediment characteristics, and depth were considered for their potential influence on the density, distribution, and biomass of conch. Field experiments were conducted to determine the role of habitat selection in natural conch distributions.

**Table 1**

Habitat characteristics of the two seagrass meadow study sites. Units for each are: depth (meters at low water), sediment grain size (Ø), organics (% dry wt), *Thalassia shoots* (n/m²), *Thalassia* and detritus biomass (g dry wt/m²). Values are means ± SD. $n$ = number of measurements from three transects.

| | Stations | | | | | | |
|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
| **Children's Bay Cay** | | | | | | | |
| Depth ($n$ = 3) | 1.0±0.1 | 1.2±0.1 | 1.8±0.2 | 2.7±0.3 | 3.4±0.3 | – | – |
| Sediment grain size ($n$ = 3) | 1.50±0.11 | 1.38±0.31 | 1.50±0.07 | 1.83±0.59 | 2.44±0.51 | – | – |
| Organics ($n$ = 3) | 2.44±0.20 | 2.35±0.25 | 2.61±0.06 | 2.98±0.44 | 3.88±0.45 | – | – |
| **July** | | | | | | | |
| *Thalassia* shoots ($n$ = 6) | 0.0±0.0 | 64.0±16.0 | 304±48.0 | 576±48.0 | 704±80.0 | – | – |
| *Thalassia* biomass ($n$ = 6) | 0.0±0.0 | 3.5±1.1 | 16.0±4.7 | 48.0±4.8 | 65.6±14.4 | – | – |
| Detritus ($n$ = 6) | 0.0±0.0 | 0.80±0.80 | 3.68±1.9 | 30.9±18.6 | 104±44.8 | – | – |
| **February** | | | | | | | |
| *Thalassia* shoots ($n$ = 6) | 0.0±0.0 | 67.2±19.2 | 304±72.0 | 736±208 | 864±160 | – | – |
| *Thalassia* biomass ($n$ = 6) | 0.0±0.0 | 8.6±9.9 | 13.9±4.6 | 56.0±20.8 | 80.0±19.2 | – | – |
| Detritus ($n$ = 6) | 0.0±0.0 | 0.64±0.80 | 0.64±1.28 | 48.0±36.8 | 125±96.0 | – | – |
| **Shark Rock** | | | | | | | |
| Depth ($n$ = 3) | 1.6±0.1 | 1.7±0 | 2.0±0 | 2.5±0.1 | 2.8±0.1 | 3.3±0.3 | 3.2±0.1 |
| Sediment grain size ($n$ = 3) | 1.58±0.06 | 1.68±0.21 | 1.96±0.18 | 2.00±0.13 | 2.20±0.35 | 2.57±0.01 | 2.53±0.10 |
| Organics ($n$ = 3) | 2.44±0.03 | 2.33±0.22 | 2.34±0.12 | 2.70±0.11 | 3.21±0.22 | 3.57±0.46 | 2.85±0.47 |
| **July** | | | | | | | |
| *Thalassia* shoots ($n$ = 6) | 0.0±0.0 | 72.0±12.8 | 256±44.8 | 528±46.4 | 669±56.0 | 741±88.0 | 728±123 |
| *Thalassia* biomass ($n$ = 6) | 0.0±0.0 | 5.28±1.4 | 20.3±4.6 | 54.4±8.0 | 62.4±14.4 | 83.2±1.6 | 97.6±20.8 |
| Detritus ($n$ = 6) | 0.0±0.0 | 0.48±0.64 | 3.2±2.7 | 13.8±13.1 | 64.0±22.4 | 96.0±40.0 | 176±41.6 |
| **February** | | | | | | | |
| *Thalassia* shoots ($n$ = 6) | 0.0±0.0 | 68.8±19.2 | 292±81.6 | 452±54.4 | 608±101 | 816±217 | 764±128 |
| *Thalassia* biomass ($n$ = 6) | 0.0±0.0 | 6.9±4.8 | 36.8±17.6 | 68.8±33.6 | 78.4±14.4 | 80.0±9.6 | 115±36.8 |
| Detritus ($n$ = 6) | 0.0±0.0 | 8.0±1.1 | 1.3±1.9 | 14.7±15.4 | 157±35.2 | 84.8±4.8 | 309±174 |

## Site description

This study was conducted in the Exuma Cays, Bahamas, at two sites characterized by turtlegrass *Thalassia testudinum* König and known juvenile queen conch populations (Wicklund et al. 1988). The first site (CBC) was located 1.5 km west of Children's Bay Cay (23° 44.3′N, 76°04.5′W). The second site (SR) was located just southwest of Shark Rock (23°45.0′N, 76°07.5′W), a rock outcrop off the southern end of Norman's Pond Cay. There is a gradient in depth at both sites from a shallow sand bar (<1.0 m) to a depth of approximately 3.5 m, accompanied by a gradient in seagrass and detritus biomass (Table 1). Tidal range in the area is approximately 1 m and both sites are subject to strong reversing tidal currents, sometimes exceeding 50 cm/second.

Conch density was highest (~2.0/m²), near the population centers, decreasing in density towards their peripheries. At each site three transects were made, each separated by approximately 50 m. Divers were towed by a small boat around each site to place buoys on the edges of each population. Transects were then positioned through the population centers, parallel to the depth gradient. Transect lengths were an average of 61 m at CBC and 142 m at SR. Stations marked by stakes were placed along each transect (5 for CBC and 7 for SR) from bare sand to the highest density seagrass. *Thalassia* shoot density was used to set all stations of equivalent number in similar habitats for both sites. Station 1 of each transect was placed on bare sand, with no seagrass or detritus. Stations 2, 3, 4, and 5 were placed in the following approximate shoot densities, respectively: 70, 300, 550, and 700 shoots/m². Stations 6 and 7 at SR were characterized primarily by increasing accumulated detritus and higher seagrass biomass and not increasing shoot density.

## Methods and materials

### Field measurements

Counts were made in July 1988 and February 1989 to test for seasonal differences in conch distribution. In February at CBC we found that the center of the population had moved north of its July location, and

so transect 1 (the southernmost transect) was moved between transects 2 and 3 for the February sampling. Measurements, including station depth, conch density and shell lengths, macrophyte shoot density and biomass, and amount of macroscopic detritus, were taken at each station along the transects within a circle of 2.5 m radius around each stake. Sediment grain-size and organic content were measured in July 1988.

Depths were measured at low water using an electronic depth sounder on a 17-foot Boston Whaler, adjusting for the depth of the transducer below the surface. Using scuba, conch were gathered within each 2.5-m circle at each station, counted, and measured for shell length using large calipers.

A separate collection of 80 conch ranging from 17 to 196 mm in siphonal length was made to generate a length-weight curve. After freezing, the conch were extracted from their shells, washed to remove feces, blotted to remove excess water, and weighed. The following equation describes the significant correlation ($r^2 = 0.987$, $F = 5233.4$, $p<0.001$) between shell length and wet weight:

$$\log_{10}(\text{wet weight}) = 3.403 \times \log_{10}(\text{length}) - 5.569$$

The equation was used to convert length-frequency data to biomass values.

Two replicate samples of macrophytes and macroscopic detritus (mostly senescent seagrass blades and debris) were collected at each station by haphazardly placing a quadrat with 25-cm sides within each circle. The number of shoots within the quadrat were counted and then collected along with the macrophyte detritus into nylon bags (3.0-mm mesh). *Thalassia* blades (using only aboveground parts), and macrodetritus were separated in the laboratory and dried at 80°C for approximately 24 hours to constant weight. Dry-weight biomass was determined for the individual components.

A core of 40 mm diameter, with a penetration depth of 5 cm, was taken for determination of sediment grain-size distribution and organic content. A subsample of approximately 100 g wet weight was dried at 80°C to constant mass and incinerated at 550°C for 4 hours to determine sediment organic content. Organic content was quantified as the percent difference between dry weight and ash-free dry weight. Another sediment subsample of approximately 50 g was used to determine sediment grain-size. After washing to remove salts and to extract the silt-clay fraction, sand-sized particles were analyzed using standard Ro-Tap procedures. Silt-clay fractions were analyzed using standard pipet procedures (Folk 1966). Product moment statistics were generated for mean grain size and sortedness (McBride 1971).

## Habitat preference experiments

Experimental manipulations of plots of seagrasses were made at the Shark Rock site to test for habitat preference in conch of various size classes. Cages 3.6 m diameter (10.2 $m^2$) were constructed of black plastic mesh with 20-mm openings. The cages were 25 cm high and supported by 1-m long pieces of reinforcement bar driven into the sediment. The bottom edge of the screen was pushed into the sediment approximately 3 cm to prevent escape of conch. No losses occurred during the experiments.

Four cages were built in locations similar to station 5 (see above), characterized by *Thalassia* shoot densities of 700 shoots/$m^2$ (Moderate Density). Two cages were built near stations 3 with approximately 300 shoots/$m^2$ (Low Density), and two cages were built in high biomass habitats similar to station 7 with approximately 750 shoots/$m^2$ plus a heavy layer of detritus (High Density). Macrophytes in two of the moderate-density cages were manipulated so that one-half of each was reduced to 300 shoots/$m^2$ (Low Density) (Table 2). This was accomplished by placing a rope across the cage through the center and parallel to the direction of flood tide current. (Manipulations were oriented with the current because juvenile conch at the study site are known to move either up or down current during migration.) Then shoots were systematically pulled from one-half of the cage to achieve the desired shoot density. The two cages for this Moderate/Low treatment were manipulated to provide mirror images of one another. The other two moderate-density plots were manipulated in a similar fashion to provide Moderate/Sand treatments, where all seagrass shoots were removed from one side of each cage. Replicate Low/Sand treatments were constructed by manipulating the two low-density plots. High/Moderate treatments were set up by manipulating the high-density plots. About 80% of the loose detritus (comprised mostly of senescent seagrass blades) was removed from half of the high-density plots. Final shoot densities in the high- and moderate-density areas were similar (656 and 672 shoots/$m^2$, respectively), and removal of detritus yielded a macrophyte environment similar to the moderate-density areas (Table 2). The manipulations required maintenance such as removing new growth and accumulated detritus. Except for the removal of detritus which accumulated along the edges of the cages, maintenance of the plots was performed between the short habitat preference runs.

Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

**Table 2**

Summary of biological conditions presented in experiments of habitat preference in queen conch. There were no significant differences between plots in any of the four treatment levels (ANOVA, $p>0.05$).

| Treatment | $n$ | Seagrass shoots ($n/m^2$) | Seagrass biomass (g dry wt/$m^2$) | Detritus (g dry wt/$m^2$ |
|---|---|---|---|---|
| Sand | 8 | 0±0 | 0±0 | 0±0 |
| Low Density | 8 | 272±32 | 27±13 | 3.0±3.5 |
| Moderate Density | 12 | 672±80 | 72±20 | 58±37 |
| High Density | 4 | 656±64 | 98±11 | 269±66 |

Between 27 September and 28 October 1988 three conch size-classes were tested for their preferences for habitat type. The classes included animals between 75 and 100 mm shell length (~1 year old), conch between 125 and 150 mm (2 and 3 years old), and adults with the fully developed flare of the shell lip (~4 years or more). All were collected from the seagrass beds around the experimental enclosures. To provide a conch density similar to that in nature, 10 juveniles of a size-class were added to each enclosure (1.0 conch/$m^2$) after removal of all large invertebrates such as urchins, hermit crabs, and conch. For runs with the adults, 8 animals were placed in an enclosure.

Preliminary experiments showed that the distribution of conch in both Moderate/Low and Moderate/Sand treatments did not change significantly between 1 and 5 days; therefore, all runs were terminated at 3 days. At the end of a run, the numbers of conch found on each side of the cage were recorded, and the animals were removed. Because the animals touching the screen may have been moving around the periphery of the enclosure, they were not included in the counts. Three or four runs were made for each size-class and treatment, except those in the High/Moderate enclosures where two runs were made in each cage. No significant differences were found in the distribution of animals in a size-class in any of the pairs of cages providing similar combinations of macrophytes (Fisher's Exact Test, $p>0.05$); therefore, the paired cages were considered to be replicates.

## Results

### Station characteristics

Average depths for the five stations at CBC increased from station 1 (1.0 m) to station 5 (3.4 m). Average station depths for SR increased from station 1 (1.6 m) to station 6 (3.3 m) and then decreased slightly at station 7 (3.2 m). *Thalassia* shoot density, biomass, and detritus biomass all increased with increasing station number and depth, with a few exceptions (see Table 1). At CBC shoot density ranged from 0.0 to 864 shoots/$m^2$, *Thalassia* biomass from 0.0 to 80 g dry wt/$m^2$, and detritus biomass from 0.0 to 125 g dry wt/$m^2$. At SR shoot density ranged from 0.0 to 765 shoots/$m^2$, *Thalassia* biomass from 0.0 to 115 g dry wt/$m^2$, and detritus biomass from 0.0 to 309 g dry wt/$m^2$.

Sediment grain-size at the CBC transects was relatively constant (1.38–1.83 $\phi$) between stations 1 and 4, but finer at station 5 (2.44 $\phi$). Sediment organic content increased slightly over the transects from low-biomass to high-biomass stations. At the SR transects mean grain diameter decreased (increasing $\phi$) from stations 1–6, while stations 6 and 7 had nearly equal grain size (2.57 and 2.53 $\phi$). Organic content was highest at SR station 6, but values ranged only from 2.33 to 3.50% of dry sediment weight.

Children's Bay Cay and the Shark Rock site showed highly significant correlations among all of the variables: water depth, seagrass shoot density, aboveground seagrass biomass, and standing crop of macrodetritus (Table 3). Weakest correlations ($r = 0.586$ to 0.631) occurred between detritus and the other variables at Shark Rock in February, when abundance of detritus was low. Correlations between macrophyte and depth characteristics remained highly significant when all sites, stations, and dates were included in regression models (Table 3) suggesting that the relationships are relatively universal in the study area. The highest correlation occurred between seagrass shoot density and water depth ($r = 0.930$), and weakest correlations were found between detritus biomass and the other variables.

### Conch density patterns

At CBC there was an increase in conch density in both July and February along the transects from station 1–5, except for a small decrease in February from station 4 to station 5 (Fig. 1). Densities in July were similar

**Table 3**

Pearson correlation matrices showing the relationships among depth and macrophyte variables at the seagrass meadow study sites. The upper and lower sections of the first two matrices are for July and February collections, respectively. The bottom matrix is for all stations and dates combined. Shoots = density of *T. testudinum* shoots; *Thalassia* = biomass of *T. testudinum*; Detritus = biomass of macrodetritus.

| | Depth | Shoots | *Thalassia* | Detritus |
|---|---|---|---|---|
| | | **Children's Bay Cay** | | |
| Depth | — | 0.966** | 0.938** | 0.911** |
| Shoots | 0.968** | — | 0.961** | 0.817** |
| *Thalassia* | 0.873** | 0.880** | — | 0.839** |
| Detritus | 0.728** | 0.752** | 0.826** | — |
| | | **Shark Rock** | | |
| Depth | — | 0.969** | 0.964** | 0.839** |
| Shoots | 0.950** | — | 0.954** | 0.769** |
| *Thalassia* | 0.877** | 0.891** | — | 0.889** |
| Detritus | 0.631* | 0.586* | 0.623* | — |
| | | **Combined sites and dates** | | |
| Depth | — | | | |
| Shoots | 0.930** | — | | |
| *Thalassia* | 0.871** | 0.887** | — | |
| Detritus | 0.648** | 0.628** | 0.726** | — |

*$p<0.05$; ** $p<0.01$.

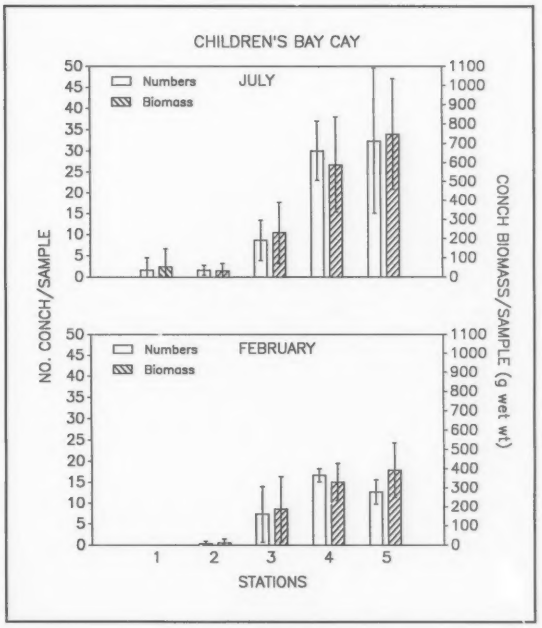


**Figure 1**

Number of conch and conch biomass sampled within a 2.5-m radius circle at Children's Bay Cay, July 1988 and February 1989, at each station. Values are means ± SD.

to those in February at stations 1, 2, and 3. Stations 4 and 5 had densities almost twice as high in July as those in February. At SR, the general pattern was an increase in conch density from station 1–5 (except a small decrease in July at station 4) (Fig. 2). In July, the density then decreased sharply at stations 6 and 7. In February, the density increased further at station 6 and then decreased at station 7. More pronounced than at CBC, the densities at SR in February at stations 3, 4, and 5 were lower than the July densities.

After log transformation of the data to improve heterogeneity in the variance, a multi-way ANOVA was used to test for differences and interactions in conch density between sites, dates, transects, and stations (Table 4). Transects were examined as blocks, and hence there were no interaction terms with transect. Since SR had 7 stations as opposed to 5 at CBC, stations 6 and 7 at SR were not used in this analysis where CBC and SR were compared.

There were no significant interaction terms or block (transect) effects in the ANOVA ($p>0.05$); therefore, the effects of date, site, and station may be interpreted directly. It is clear from Figures 1 and 2 that conch densities were higher in July than in February at both CBC and SR at most stations. Significant site effects appear to be related to the low numbers of conch at SR, particularly in February and at station 1–3. Station effects occurred because of the increase in conch

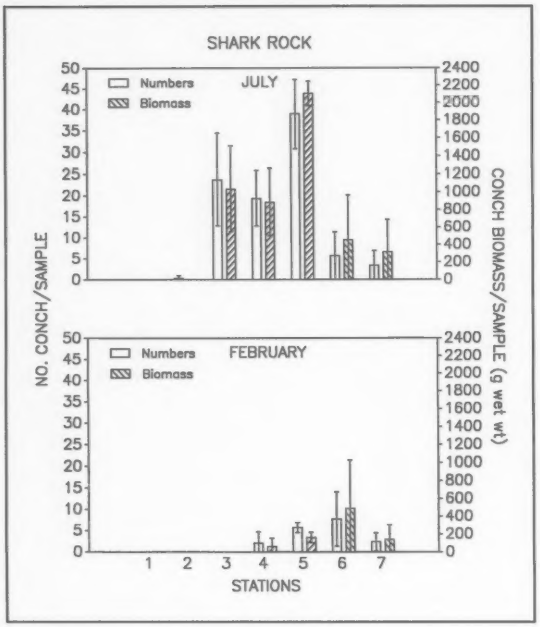


**Figure 2**
Number of conch and conch biomass sampled within a 2.5-m radius circle at Shark Rock, July 1988 and February 1989, at each station. Values are means ± SD.

**Table 4**
Results of multi-way analysis of variance for conch density in seagrass meadows. Data were log-transformed and transects were examined as blocks.

| Source | df | MS | $F$ | $p$ |
|---|---|---|---|---|
| Date | 1 | 2.503 | 22.755 | <0.0001 |
| Site | 1 | 0.753 | 6.846 | 0.011 |
| Transect | 2 | 0.032 | 0.289 | 0.750 |
| Station | 6 | 2.400 | 21.820 | <0.0001 |
| Date * Site | 1 | 1.047 | 3.058 | 0.086 |
| Date * Station | 6 | 0.539 | 1.574 | 0.171 |
| Site * Station | 6 | 0.160 | 0.468 | 0.829 |
| Date * Site * Station | 6 | 0.228 | 0.642 | 0.696 |
| Error | 56 | 0.355 | | |

**Table 5**
Results of multi-way analysis of variance for conch biomass in seagrass meadows. Data were log-transformed and transects were examined as blocks.

| Source | df | MS | $F$ | $p$ |
|---|---|---|---|---|
| Date | 1 | 9.349 | 15.564 | <0.0001 |
| Site | 1 | 3.025 | 5.036 | 0.028 |
| Transect | 2 | 0.155 | 0.258 | 0.773 |
| Station | 6 | 11.511 | 19.162 | <0.0001 |
| Date * Site | 1 | 3.838 | 2.372 | 0.129 |
| Date * Station | 6 | 1.868 | 1.154 | 0.343 |
| Site * Station | 6 | 1.614 | 0.997 | 0.436 |
| Date * Site * Station | 6 | 1.032 | 0.610 | 0.722 |
| Error | 56 | 1.692 | | |

density between stations 1 and 5 at all sites and dates, except SR station 4.

A one-way ANOVA and a Newman-Keuls multiple range test were used to test for differences in log transformations of conch density among stations 1–5 combining all sites and dates (CBC–July, SR–July, CBC–February, SR–February). There was a significant difference between stations ($F = 22.02$, $p<0.0001$). Conch densities increased with increasing station number, ranging from 0.42 (±1.38) to 22.4 (±15.8). Newman-Keuls tests showed that the logs of conch density at stations 1 and 2 were significantly different from all other stations, though not from one another, as were stations 4 and 5. Station 3 was significantly different from all other stations (Newman-Keuls, $p<0.05$).

## Conch biomass patterns

As with conch density, there was an increase in conch biomass at CBC, from stations 1 to 5. The pattern was strong for both July and February, although the actual biomass values were higher in July at stations 4 and 5 than in February. At SR the biomass also increased from stations 1 to 5 (with a slight decrease at station 4 in July). In July, biomass decreased sharply at station 6 and 7, while in February the biomass continued to increase at station 6 and decreased at station 7. In July stations 3, 4, and 5 had much higher biomass values than in February.

After log transformations of the biomass data, a multi-way ANOVA was used again to test for differences or interactions between dates, sites, transects, and stations in conch biomass with transects examined as blocks (Table 5). Where CBC and SR were compared, stations 6 and 7 at SR were not used.

There were no significant interaction terms and no block effects on the ANOVA ($p>0.05$), therefore the effects of date, site, and station are interpreted directly. As mentioned above, conch biomass at both CBC and SR was higher in July than in February at most stations. Site differences appear to be due to low biomass values in February at SR, especially at stations 1–3. Station differences clearly resulted from the increase of conch biomass with the increase in station number, at all sites and dates, except SR station 4.

**Table 6**

Pearson correlation coefficients for relationships between measures of conch abundance and characteristics of seagrass habitat for different months and sites. CBC = Children's Bay Cay site; SR = Shark Rock site. At the Shark Rock site, analyses were made with 5 and 7 stations because of decreasing numbers of conch at stations 6 and 7 (see text).

| | CBC July | CBC Feb. | SR (5 stations) July | SR (5 stations) Feb. | SR (7 stations) July | SR (7 stations) Feb. |
|---|---|---|---|---|---|---|
| | | | **Conch density** | | | |
| Depth | 0.868** | 0.868** | 0.813** | 0.837** | 0.168 | 0.650** |
| Shoots | 0.860** | 0.851** | 0.831** | 0.787** | 0.314 | 0.726** |
| *Thalassia* | 0.910** | 0.753** | 0.779** | 0.803** | 0.141 | 0.495* |
| Detritus | 0.608* | 0.753** | 0.701** | 0.853** | 0.141 | 0.495* |
| | | | **Conch biomass** | | | |
| Depth | 0.774** | 0.892** | 0.850** | 0.801** | 0.216 | 0.530* |
| Shoots | 0.874** | 0.831** | 0.863** | 0.741** | 0.423 | 0.634** |
| *Thalassia* | 0.886** | 0.781** | 0.836** | 0.799** | 0.270 | 0.353 |
| Detritus | 0.680** | 0.597* | 0.827** | 0.780** | 0.004 | 0.244 |

| | Combined sites and dates (5 stations) | |
|---|---|---|
| | **Conch density** | **Conch biomass** |
| Depth | 0.603** | 0.492** |
| Shoots | 0.636** | 0.513** |
| *Thalassia* | 0.518** | 0.438** |
| Detritus | 0.330* | 0.266* |

*$p<0.05$; **$p<0.01$.

A one-way ANOVA and a Newman-Keuls multiple range test were used to test for differences in log transformations of conch biomass among stations for all date-site samples. There was a significant difference in the log of conch biomass across stations. Conch biomass increased from 13.4 g wet weight (±44.5) at station 1 to 851 g wet weight (±766) at station 5. The log of conch biomass at stations 1 and 2 were not different from one another but were each significantly different from stations 3, 4, and 5. Stations 3 and 5 were each significantly different from all stations but station 4 (Newman-Keuls, $p<0.05$).

## Relationships between conch and the independent variables

There were highly significant correlations between both density and biomass of conch in the field and the depth and macrophyte characteristics of the habitat (Table 6). Tested by individual date at Children's Bay Cay, correlations between conch density and depth, shoot density, and seagrass biomass were high and relatively similar ($r$ values between 0.753 and 0.910), while correlations with detritus were significant but lower. Similar patterns held for conch biomass. At Shark Rock in July, conch numbers and biomass were highest at station 5 (Fig. 2) and did not increase over the entire range of seagrass shoot density or biomass. Therefore, linear regressions of conch density and biomass with depth and macrophyte characteristics did not yield high or significant correlations in most cases when data from all seven stations were included (Table 6). Highly significant correlations were found using the first five stations; all of the habitat characteristics yielded correlation coefficients between 0.701 and 0.863 (Table 6).

In regression models including data from all dates, sites, and stations 1–5, all of the environmental variables yielded significant correlations with conch density and biomass (Table 6). Highest correlations occurred between seagrass shoot density and both conch density and conch biomass. Lowest correlation coefficients occurred with detritus.

Two stepwise multiple regressions were run to determine the best multiple regression models for conch density and conch biomass using all of the data for stations 1–5 (all dates and sites combined). Alpha to enter and remove from the models was set at 0.150. The regression model for conch density included first shoot density followed by detritus standing crop, and yielded a

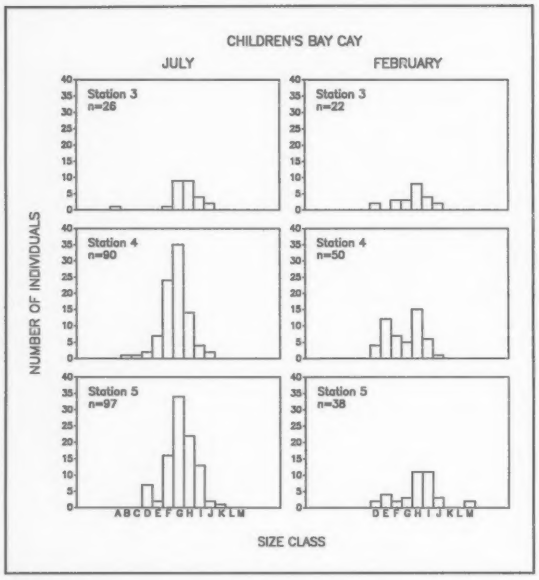


**Figure 3**

Number of individuals per sample (2.5-m radius circle) within each conch size-class for each station at Children's Bay Cay, July 1988 and February 1989. Size-classes are as follows: A = 40–49 mm, B = 50–59 mm, C = 60–69 mm, D = 70–79 mm, E = 80–89 mm, F = 90–99 mm, G = 100–109 mm, H = 110–119 mm, I = 120–129 mm, J = 130–139 mm, K = 140–149 mm, L = 150–159 mm, M = 160–169 mm, N = 170–179 mm, O = 180–189 mm, P = 190–199 mm, and Q = 200–209 mm.

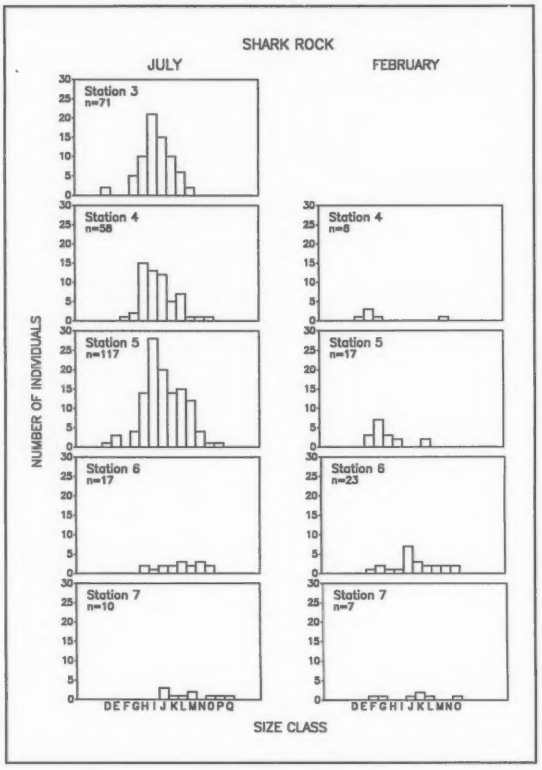


**Figure 4**

Number of individuals per sample (2.5-m radius circle) within each conch size-class for each station at Shark Rock, July 1988 and February 1989. For size-classes see Figure 3.

multiple correlation coefficient of 0.664 ($p<0.001$). The stepwise multiple regression model for conch biomass included only shoot density and provided a multiple regression coefficient of 0.513 ($p<0.001$). No other variables contributed significantly to the correlation.

Results of the regressions and the Newman-Keuls tests for conch density across stations indicate that stations 3–5 provide a suitable habitat for conch larger than 70 mm SL with habitat characteristics ranging as follows: 256–864 mean shoots/m$^2$, 13.9–80.6 mean g dry wt of *Thalassia*/m$^2$, and 0.64–157.12 mean g dry wt of detritus/m$^2$. In addition, the correlation between conch and macrophyte characteristics are linear only up to station 5 (608–864 mean shoots/m$^2$, 62.4–80.6 mean g dry wt of *Thalassia*/m$^2$, 64.0–157.1 mean g dry wt of detritus/m$^2$) which appears to be the near-optimal habitat for juvenile conch larger than 70 mm.

## Conch length-frequency patterns

The Kolmogorov-Smirnov two-sample test was used to test for significant differences in the length-frequency distribution of conch at different stations. Only stations with at least 10 conch were used in the analysis (CBC stations 3–5 in both July and February; SR stations 3–7 in July and stations 5–6 in February).

In July, CBC stations 3, 4, and 5 all had significantly different conch length-frequencies (stations 3 and 4, $p<0.0001$, stations 3 and 5, $p=0.015$, stations 4 and 5, $p<0.0001$). Mean lengths varied only from 102 to 111 mm, and the statistical differences were a result of subtle differences in the shape of the distributions (Fig. 3). In February at CBC, the length-frequency distribution of conch at station 3 was different significantly from that at station 4 ($p=0.004$), and the distribution at station 4 was different significantly from that at station 5 ($p<0.0001$). The length-frequencies at stations 3 and 5 were not different ($p=0.062$); the mean values and shapes of the distribution were similar (Fig. 3).

In July, conch length-frequency patterns at SR stations 3, 4, and 5 were not different (stations 3 and 4, $p=0.220$; stations 4 and 5, $p=0.260$), and had means

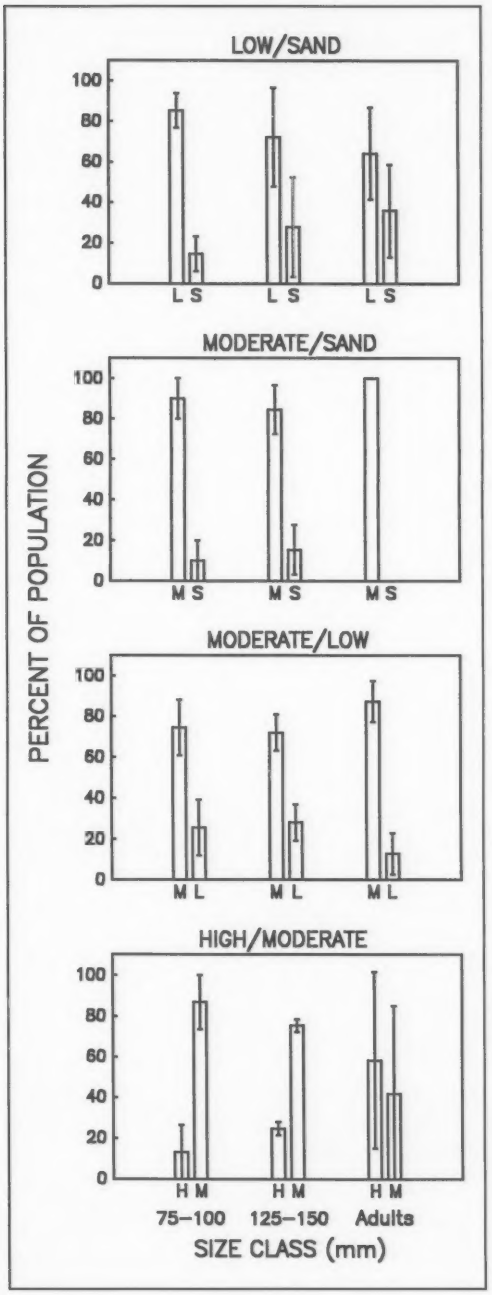


**Figure 5**
Percentage of conch in three size-classes found within a habitat type from a choice of two types. Choices included combinations of bare sand, low and high seagrass biomass.

**Table 7**
Results of *G*-tests on habitat choice by three size-classes of conch presented with paired habitats.

| Size-class (mm) | No. of runs | Total no. of conch in the habitats | $G_{adj}$ | $p$ |
|---|---|---|---|---|
| **Low/Sand treatments** | | | | |
| 75–100 | 6 | 37/6 | 24.86 | <0.01 |
| 125–150 | 6 | 28/9 | 10.24 | <0.01 |
| Adults | 6 | 6/5 | 0.09 | >0.05 |
| **Moderate/Sand treatments** | | | | |
| 75–100 | 6 | 53/7 | 42.99 | <0.01 |
| 125–150 | 8 | 61/10 | 36.41 | <0.01 |
| Adults | 6 | 33/0 | | <0.01 |
| **Moderate/Low treatments** | | | | |
| 75–100 | 6 | 44/17 | 12.27 | <0.01 |
| 125–150 | 6 | 38/22 | 9.72 | <0.01 |
| Adults | 6 | 31/5 | 20.89 | <0.01 |
| **High/Moderate treatments** | | | | |
| 75–100 | 4 | 2/23 | 20.72 | <0.01 |
| 125–150 | 4 | 8/25 | 9.19 | <0.01 |
| Adults | 4 | 4/3 | 0.14 | >0.05 |

between 129 and 136 mm. Distributions at stations 6 and 7 were not different ($p = 0.749$) (Fig. 4). This pattern of size-frequency distribution showed that, in July, conch were significantly larger at the stations with higher macrophyte biomass (stations 6 and 7), while smaller conch were found at sites with moderate-to-low seagrass biomass (stations 3, 4, and 5). In February, the two SR stations with more than 10 conch—stations 5 and 6—had significantly different length-frequencies ($p<0.0001$) (Fig. 4). Again, the large conch were associated with high seagrass biomass.

## Habitat preference experiments

Results of the habitat preference experiments showed that conch were proficient in detecting and choosing habitats with different macrophyte characteristics (Fig. 5). Of the conch in all size classes, 90% were associated with the moderate density plots as opposed to sand habitat (10%). Habitat selectivity was less strong in the other habitat pairs, but it is clear that plots with seagrass present were selected over bare-sand habitats, and moderate-density seagrass was selected over either high- or low-density seagrass.

Heterogeneity *G* tests showed that the results of runs within all of the individual habitat preference tests were homogeneous ($p<0.05$) except one (Low vs. Sand; 125–150 mm; $G_H = 14.37$, $p>0.05$). Standard *G* tests were used with the pooled data to test the null hypothesis that animals were distributed equally over

the two sides of the enclosures. All treatments and size-classes resulted in highly significant differences ($p<0.01$), except for two cases (Table 7). Adults in the Low/Sand treatment and adults in the High/Moderate treatment showed no significant habitat preference ($p>0.05$). In these two experiments adult conch were highly motile, and more than 50% of the individuals were found traveling around the walls of the enclosures. Because only animals not touching the walls were included in the analysis, the numbers for analysis were small and highly variable (Table 7, Fig. 5). Where a high-preference habitat (Moderate Density) was paired with a low-preference habitat (Low Density or Sand), adult conch were not found against the walls of the enclosures in such high numbers (28%) and habitat selection was highly significant (Table 7).

## Discussion

Many marine organisms are known to prefer seagrass beds over bare sand. For example, amphipods, tanaidaceans, decapods, and fishes have all been found to be more abundant in seagrass beds than on bare sand (Heck and Thoman 1981, Holt et al. 1983, Stoner 1983, Heck et al. 1989). Also, abundance of animals within seagrass beds appears to be influenced strongly by the local amount of macrophyte structure. Numbers of both decapod and peracarid crustaceans have been correlated with seagrass biomass (Heck and Orth 1980, Stoner 1980a, Lewis 1984). A direct linear relationship between seagrass biomass and harpacticoid abundance and diversity was attributed to an increase in habitable space, nutritional resources, and reduced levels of predation (Hicks 1980). Communities of epibenthic fish on the banks of Florida Bay were associated with areas of high seagrass biomass and with accumulations of seagrass detritus (Sogard et al. 1987). Detritus was thought to provide a rich food source as well as a refuge from predators.

The general association of queen conch with turtlegrass *Thalassia testudinum* is well known (Randall 1964, Hesse 1979, Weil and Laughlin 1984), but quantitative relationships between the mollusc and seagrass beds are reported for the first time in this study. The distributional patterns of queen conch near Lee Stocking Island were similar to patterns found for other taxa, with few individuals associated with bare sand and low-density seagrass. As was true for other species, juvenile conch densities increased with macrophyte biomass and shoot density over a wide range; however, optimal levels of macrophyte cover were found, beyond which only larger individuals were associated. The observed association of juvenile queen conch with moderate amounts of macrophyte cover (shoot density, biomass, etc.) probably results from a combination of mechanisms: (1) a simple inability of the animals to maneuver into or through heavy stands of seagrass and detritus, (2) active habitat choice for specific seagrass cover, and (3) differential survivorship associated with different macrophyte densities, especially in the smaller size-classes.

The upper limit of seagrass density with which juvenile queen conch are associated is probably set by their locomotory abilities. Randall (1964) speculated that thick stands of seagrass obstruct the movements of small conch. High shoot density is also responsible for heavy accumulations of detritus and soft sediments which may impede locomotion. Given that queen conch propel their heavy shells with thrusts of a pointed operculum on the end of a muscular foot, locomotion is most efficient on a firm substratum.

The direct relationship between conch density and seagrass density below the optimal level is most likely linked to more complex interactions. It is known that abundance of food can be limiting for juvenile conch in the field at natural density (Stoner 1989). The primary sources of food for juvenile conch in nursery habitats are macrodetritus and algal epiphytes (Stoner and Waite, In review); both of these food items increase with seagrass density. Blade and detritus productivity increase with shoot density, and seagrasses have the effect of increasing the entrapment of fine sediments and detritus (den Hartog 1967, Orth 1977, this study), useful only up to the point of impeded locomotion. Algae consumed by conch in the seagrass nursery areas are primarily those growing as epiphytes on *Thalassia* blades. Production of these epiphytes can be as high as 50% of the seagrass production (den Hartog 1979), and increases with seagrass shoot density. The increase in density of conch with seagrass shoot density, therefore, may be a function of habitat choice by individuals for areas with greater abundance of foods and/or a function of food limitation in the population.

The relationship between conch density and seagrass shoot density can also be a response to predation. This response could be direct, whereby the survivorship of conch increases with increasing seagrass structure, or indirect, where habitat preference for high-structure habitats has evolved as a response to predators. In either case, the role of seagrass biomass in protecting prey species is known for a wide variety of predator-prey combinations (Coen et al. 1981, Stoner 1982, Leber 1985, Heck and Wilson 1987), and experiments with crustaceans have shown that prey species are proficient in choosing high-density seagrass (Stoner 1980b, Coen et al. 1981, Bell and Westoby 1986). The fact that small conch were more proficient in selecting habitats of particular seagrass biomass or shoot density than

large individuals suggests that there is strong selective pressure for habitat choice in small conch, probably via size-specific mortality. Susceptibilty of juveniles to predation is known to decrease with increasing conch size (Appeldoorn 1984).

Whether the observed distributional patterns are ultimately a response to foods and/or predators cannot be determined from data presented here; however, new experiments using artificial structures and predator manipulations would be useful. In any case, strong habitat preferences suggest that evolved behavioral mechanisms are influential, and the evolution of habitat choice in conch is probably related to both procurring sufficient foods and avoiding predators.

Significant effects of date in the density and biomass of conch in the seagrass beds was related to the normal seasonality of reproduction and recruitment in conch of the Exuma Cays. The 1+ year-class (~40–100 mm), spawned during the previous summer (1987), was most abundant in July. In the Exuma Cays, spawning occurs between April and October (Stoner et al. In review), with greatest recruitment to the benthos probably occurring between August and October. Juvenile conch spend most of their first year buried in the sediment; therefore, only the 1987 and older cohorts were surveyed in July 1988 and February 1989. In February, the 1988 cohort had not yet emerged from the sediment and, therefore, the 1+ year-class was not found in that survey.

Information on the settlement and distribution of juvenile conch in their first year of life will be particularly useful in elucidating mechanisms of distribution and abundance. Conch less than 40 mm have been found in very shallow, unvegetated subtidal sediments, moving to deeper waters or seagrass beds with age (Weil and Laughlin 1984; Stoner and Sandt, unpubl. data). Highest abundance of 1-year-old conch in sparse seagrass close to sand shoals, therefore, could be a result of ontogenetic migration.

The relationship between juvenile conch and easily measured characteristics of the macrophyte community should prove useful in predicting conch distributions and in planning stock-enhancement programs involving the seeding of hatchery-reared conch. The lack of statistical interaction among the factors site, station, and date suggests that the strong relationships between conch and seagrass shoot density (and other macrophyte characteristics) are relatively universal. It must be pointed out, however, that the surveys were conducted within areas known to be long-term conch nursery sites, and there are extensive areas of seagrasses on the Exuma Bank near Lee Stocking Island which appear to have similar habitat characteristics but no resident conch populations. Recent transplant experiments have shown that many of the habitats with appropriate seagrass, sediment, and detritus characteristics do not provide good growth or survivorship in juvenile conch (Stoner and Sandt, In press). Clearly, there are unmeasured variables in the seagrass meadows which are important aspects of habitat quality for conch. Habitats without natural conch populations, which produced good growth and survival rates, may be recruitment limited. Such limitation may be a function of larval supply or ontogenetic movements in the species. This study demonstrates that there is a strong relationship between conch density and biomass and the amount of seagrass structure in the habitat; however, general seagrass characteristics cannot be used as predictors of conch distribution independent of other variables such as food quality, presence of predators, hydrographic considerations, and recruitment processes.

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# Key to the Hippolytid Shrimp of the Eastern Pacific Ocean

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**Abstract.**—Seventy-two species of hippolytid shrimp (Decapoda: Crustacea: Hippolytidae) have been reported from the eastern Pacific (the Aleutians to Cape Horn). There are more species to the north of Magdalena Bay, Baja California, than in tropical or temperate waters to the south. Most species of *Eualus*, *Lebbeus*, *Heptacarpus*, and *Spirontocaris* live along the temperate coasts of North America; species of *Thor*, *Trachycaris*, and *Lysmata* are most common in warm-temperate to tropical areas, and species of *Hippolyte* range from cool to tropical regions. In the eastern Pacific, species of *Nauticaris* and *Leontocaris* have been found only in the Southern Hemisphere. An annotated key to the species, with geographic and depth range and selected synonyms, is provided.

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Members of the family Hippolytidae are among the most abundant and diverse carideans of the eastern Pacific. Hippolytids are eaten by birds and fishes, and serve as cleaners for fishes such as moray eels (Chace 1937, Limbaugh 1961, Hobson and Chess 1976, Reynolds 1977). They are common inhabitants of tidepools, kelp beds, seagrass flats, and other nearshore areas, but also range into the deeper parts of the continental shelf and slope.

The greatest diversity of species of hippolytids in the eastern Pacific is in boreal to temperate waters of the northern hemisphere (Table 1). Forty-seven species live from the Aleutian Islands to Baja California, Mexico. Among these, *Lebbeus vicinus* has the greatest range, from the Aleutians to the Gulf of California. *Hippolyte californiensis* lives from the coast of Alaska to the Gulf of California. Eighteen other species range from the Aleutians or the mainland of Alaska south to southern California, USA, or Baja California, Mexico. Twenty-one species range from the Bering Sea or the Aleutians to British Columbia, Washington, or Oregon. Two species have been reported only from Puget Sound, and four species range from the Bering Sea or the Aleutians to northern or central California. An additional six species range from central California to Baja California or the Gulf of California, Mexico.

In the Northern Hemisphere, species of *Spirontocaris*, *Heptacarpus*, *Eualus*, and *Lebbeus* are diverse. Species of the first two genera are not found in the Southern Hemisphere, while species of the latter are more diverse in the northern than in the southern hemispheres. Although no species of these genera are found off both North and South America, *Lebbeus washingtonianus* and *L. bidentatus*, and *Eualus pusiolus* and *E. dozei* are very similar and may represent pairs of disjunct sibling species.

Tropical areas of the eastern Pacific are poor in hippolytid species. *Lysmata californica* ranges from central California to the Galapagos, while *Latreutes antiborealis* ranges from the Gulf of California to Chile. *Thor algicola* and *L. antiborealis* are sibling species of *T. manningi* and *L. parvulus* of the Caribbean and warm-temperate western Atlantic. *Hippolyte zostericola*, *Trachycaris restrictus*, and *Lysmata intermedia* occur both in the eastern Pacific and in the Caribbean and tropical Atlantic. *Thor spinosus* and *Lysmata trisetacea* range from the eastern Pacific to the Indo-West Pacific, and *Thor amboinensis* is circumtropical. Only *Hippolyte williamsi*, *Heptacarpus yaldwyni*, and *Lysmata galapagensis* are endemic and distinct.

The hippolytid fauna of temperate South America is depauperate compared with that of North America. Except for *Leontocaris pacificus*, the only representative of this genus in the eastern Pacific, all of the species belong to genera present in tropical or temperate areas of the northern hemisphere. Four species of *Lebbeus* live on the continental slopes.

Hippolytids of the eastern Pacific inhabit a wide range of depths and habitats. Species of *Spirontocaris*, *Lebbeus*, and *Eualus* prefer habitats from the lowest intertidal zone to the

**Table 1**
Ranges of Hippolytid species in the eastern Pacific.

**Bering Sea, Aleutian Island or Alaskan Mainland to Southern California, USA, or Baja California, Mexico**

*Eualus avinus*
*E. barbatus*
*E. berkeleyorum*
*E. biunguis*
*E. fabricii*
*E. lineatus*
*E. macrophthalmus*
*E. pusiolus*
*E. suckleyi*
*E. townsendi*
*Hippolyte californiensis*
*H. clarki*
*Lebbeus brandti*
*L. catalepsis*
*L. grandimanus*
*L. groenlandicus*
*L. polaris*
*L. possjeticus*
*L. schrenki*
*L. vicinus*
*L. washingtonianus*
*L. zebra*
*Heptacarpus brevirostris*
*H. camtschaticus*
*H. carinatus*
*H. decorus*
*H. flexus*
*H. herdmani*
*H. kincaidi*
*H. littoralis*
*H. moseri*
*H. paludicola*
*H. pugettensis*
*H. sitchensis*
*H. stimpsoni*
*H. stylus*
*H. taylori*
*H. tenuissimus*
*H. tridens*
*Spirontocaris arcuata*
*S. holmesi*
*S. lamellicornis*
*S. ochotensis*
*S. prionota*
*S. sica*
*S. snyderi*
*S. truncata*

**Central California to Baja California**

*Heptacarpus brachydactylus*
*H. franciscanus*
*H. fuscimaculatus*
*H. palpator*
*H. pictus*
*Lebbeus lagunae*
*Lysmata californica* (south to Galapagos)

**Gulf of California to Northern Peru**

*Heptacarpus yaldwyni*
*Hippolyte williamsi*
*H. zostericola*
*Latreutes antiborealis* (south to Chile)
*Lysmata galapagensis*
*L. intermedia*
*L. trisetacea*
*Thor algicola*
*T. amboinensis*
*T. spinosus*
*Trachycaris restrictus*

**Peru–Chile**

*Lebbeus bidentatus*
*L. carinatus*
*L. scrippsi*
*L. splendidus*
*Eualus dozei*
*Leontocaris pacificus*
*Lysmata porteri*

continental slopes. Species of *Lebbeus* are the deepest eastern Pacific hippolytids, living as deep as 2824 m. Except for *Heptacarpus yaldwyni*, species of *Heptacarpus* usually range from the upper intertidal zone to the continental shelf. Species of *Hippolyte* live in shallow water with sea grasses or beds of algae. Species of *Lysmata* live in tidepools or in cracks and caves among coral or rocks from the intertidal zone to shallow subtidal areas. *Thor amboiensis* tends to associate with subtidal cnidarians. *Thor algicola*, *Thor spinosus*, *Trachycaris restrictus*, and *Latreutes antiborealis* live among algae or on subtidal bottoms of sand, rock, coral, or rubble. *Leontocaris pacificus* lives on the continental slope.

Classification of the hippolytid shrimp is in flux. According to Williams (1984), species of the family are characterized by having the first two pairs of legs chelate, the first pair not much stronger than the rest, the carpus of the second pair of legs subdivided, the eyes well developed and not covered by the carapace, and the mandibles usually deeply cleft. A recent cladistic analysis by Christoffersen (1988) splits the Hippolytidae into at least seven families and divides them among two superfamilies, the Crangonoidea and the Alpheoidea. However, this analysis did not provide familial placement for all of the genera considered to belong to the traditional family Hippolytidae and provided no key to the groups. Reinterpretation of some of the genera of hippolytids, such as *Eualus*, also is being considered by Christofferson and others.

Despite the confusion surrounding the systematic relationships among hippolytids, it seems useful to provide a key to the species. The last comprehensive key to the species of the northeastern Pacific was prepared by Rathbun (1904); the most recent extensive synonymy and list of species was included in the work of Holthuis (1947). More recent keys are available for British Columbia (Butler 1980), the Gulf of California (Wicksten 1983), and Peru (Mendez 1981). Illustrations and keys to intertidal species have been provided in accounts of the fauna of Puget Sound and adjacent areas (Kozloff 1974), California (Ricketts et al. 1985; Smith and Carlton 1975; Chace and Abbott 1980) and the Gulf of California (Brusca 1980; Kerstitch 1989). Fourteen new species have been described since 1947 (Butler 1971, 1980; Jensen 1983, 1987; Kobyakova 1967; Wicksten and Butler 1983; Wicksten and Mendez 1982; Wicksten 1984, 1986, 1987a; Zarenkov 1976).

The following key includes all hippolytid species reported from the Aleutian Islands (south of the Bering Sea) to Cape Horn, excluding the Straits of Magellan. The arrangement in the key is artificial. Geographic and depth ranges are provided. Superscript numbers in parentheses at the ends of couplets refer to notes following the key, where further information on ranges, synonyms, and species of uncertain classification can be found.

## Key to the Hippolytidae

1 Lateral surface of carapace with many scattered spines. Carpus of second pereopods with 2 segments ..... ***Trachycaris restrictus* (A. Milne-Edwards)**
Eastern Atlantic from Canary Islands to St. Helena Island, Bermudas, to Brazil, Gulf of California, Panama; 0–100 m (Wicksten 1983).

Lateral surface of carapace with at most three spines. Carpus of second pereopods with 3 or more segments ..... 2

2 Carpus of second pereopods with 3 segments. (Often associated with sea grasses or brown algae) ..... 3

Carpus of second pereopods with 4 or more segments. (Size and associations various) ..... 7

3 Rostrum deep, lamellate. Anterior margin of carapace with 10 spines. No hepatic spine ..... ***Latreutes antiborealis* Holthuis**
Gulf of California to Chile, 4–46 m (Wicksten 1983).(1)

Rostrum elongate. Anterior margin of carapace with 2 spines. One hepatic spine ..... 4

4 First antennular segment without outer distal spines ..... 5

First antennular segment with one or more outer distal spines ..... 6

5 Tip of rostrum trifid. (Usually found among giant kelp, *Macrocystis* spp.) ..... ***Hippolyte clarki* Chace**
Sheep Bay, Alaska to Cedros Island, Baja California, 0–10 m (Wicksten 1983).

Tip of rostrum bifid. (Usually found among sea grasses) ..... ***Hippolyte zostericola* (Smith)**
Massachusetts to Curacao, western Colombia, shallow subtidal (Wicksten 1989).

6 First segment of antennular peduncle with one (rarely 2) spines, rostrum of female reaching nearly as far as tip of scaphocerite ..... ***Hippolyte californiensis* Holmes**
Sitka, Alaska to Baja California; rare in Gulf of California, 0–10 m, usually among eelgrass (*Zostera* sp.) (Wicksten 1983).

First segment of antennular peduncle with 3 spines, rostrum of female reaching about to distal 1/3 of scaphocerite ..... ***Hippolyte williamsi* Schmitt**
Gulf of California to Chile, 0–10 m, among rocks and brown algae (*Sargassum* sp.) (Wicksten 1983).(2)

7 Carpus of second pereopod with 4 segments. Left second pereopod longer and stronger than right ..... ***Leontocaris pacificus* Zarenkov**
Off Chile, 600–700 m (Zarenkov 1976).

Carpus of second pereopod with 6 or more segments. Left and right second pereopods equal or nearly so ..... 8

8 Carpus of second pereopod with 6 segments. (Rostrum reaching at most to end of eye. Ranging from Gulf of California to Panama) ..... 9

Carpus of second pereopod with 7 or more segments. (Rostrum reaching end of eye or beyond, found north of Gulf of California to Chile) ..... 11

9 Supraorbital spine present. Finely striped, with large bluish-red eyespots on third abdominal tergite ..... ***Thor spinosus* Boone**
Indo-Pacific to Gulf of California, subtidal (Bruce 1976, Wicksten 1983).

Supraorbital spine absent. Translucent, mottled or spotted, without eyespots ..... 10

**10** Brightly colored with pattern of bold white spots on dark background. Anterolateral margin of carapace angular. (Symbiotic with sea anemones or corals) ..... ***Thor amboinensis*** **Heller**
Tropical Atlantic and Indo-Pacific, Cocos Island and Panama. Subtidal (Chace 1972; Abele and Patton 1976).[3]

Camouflaged, translucent to mottled like algae. Anterolateral margin of carapace rounded. (Not symbiotic with sea anemones or corals) ..... ***Thor algicola*** **Wicksten**
Gulf of California to Panama, 0–20 m (Wicksten 1987a).[4]

**11** Carpus of second pereopod with 7 segments. Flagellum of antennae not as long as body. (Color in life various, often camouflaged) ..... **12**

Carpus of second pereopod with more than 7 segments. Flagellum of antenna as long as body. (Color in life often red striped) ..... **69**

**12** More than 1 supraorbital spine ..... **13**

One or no supraorbital spines ..... **20**

**13** Rostrum with 3–4 supraorbital spines ..... **14**

Rostrum with 2 supraorbital spines ..... **15**

**14** Rostrum deep, subcircular; with 10–26 mostly small dorsal spines on rostrum proper and 3–4 dorsal carapace spines, ventral margin of third pleuron acute or bluntly pointed .....
..... ***Spirontocaris prionota*** **(Stimpson)**
Bering Sea to SW of San Carlos Point, Baja California, 4–163 m (Butler 1980).[5]

Rostrum moderately deep, with 1–3 large dorsal spines, truncate apex; pleuron of third somite rounded ..... ***Spirontocaris truncata*** **Rathbun**
Strait of Georgia to SW of San Carlos Point, Baja California, 37–92 m (Wicksten 1984).

**15** Rostrum with styliform distal projection, no process on inner surface of eyestalk. (Usually found on offshore soft bottoms) ..... **16**

Rostrum without styliform distal projection, process present on inner surface of eyestalk. (Found among rocks or soft bottoms) ..... **17**

**16** Distal projection of rostrum with 1 ventral spine; epipods on first and second pereopods. (Usually living at 150 m or less) ..... ***Spirontocaris holmesi*** **Holthuis**
Yes Bay, Alaska to San Diego, California, 24–386 m (Butler 1980).[6]

Distal projection of rostrum without ventral spine; epipods on first pereopods only. (Usually living at 150 m and deeper) ..... ***Spirontocaris sica*** **Rathbun**
Restoration Bay, British Columbia to between San Benito Islands and Cedros Island, Baja California; 88–849 m (Butler 1980, Wicksten 1987b).

**17** Pleura of first to third somites ventrally acute or bluntly pointed, dactyls of third to fifth pereopods long, slender, with acute tips ..... ***Spirontocaris lamellicornis*** **(Dana)**
Bering Sea to Santa Monica Bay, California, 3–192 m (Butler 1980, Standing 1981).

Pleura of first to third somites broadly rounded ventrally, dactyls of third to fifth pereopods short and stout with bifid tips ..... **18**

**18** Body slender to moderately stout, shell thin; epipods on first and second pereopods .....
..... ***Spirontocaris snyderi*** **Rathbun**
Queen Charlotte Islands to San Cristobal Bay, Baja California, 4–141 m (Butler 1980).[7]

Body moderately stout to stout, shell thick; epipods on first to third pereopods ..... **19**

**19** Rostrum more or less ovoid; posterior dorsal spine on carapace located near middle of carapace ..... ***Spirontocaris ochotensis*** **(Brandt)**
Bering Sea to Vancouver Island, Japan, coast of Siberia; 0–247 m (Butler 1980).

Rostrum with lower limb broader than upper; posterior dorsal spine of carapace located on posterior third of carapace ..... ***Spirontocaris arcuata*** **Rathbun**
Arctic to Sea of Japan and Strait of Juan de Fuca, 5–641 m (Butler 1980).

**20 (12)** One supraorbital spine ..... **21**

No supraorbital spine ..... **36**

**21** Epipods on only first pereopods ..... **22**

Epipods on at least first and second pereopods ..... **23**

**22** Rostrum with 6–8 dorsal spines, stylocerite not reaching end of first segment of antennular peduncle ..... ***Lebbeus vicinus vicinus*** **(Rathbun)**
North of Unalaska, Aleutian Islands, 570–750 m (Rathbun 1904).

Rostrum with 3–4 dorsal spines, stylocerite reaching end of first segment of antennular peduncle ..... ***Lebbeus vicinus montereyensis*** **Wicksten and Mendez**
Monterey Bay to Gulf of California, 954–2824 m (Wicksten and Mendez 1982).

**23** Epipods on first and second pereopods ..... **24**

Epipods on at least first to third pereopods ..... **28**

**24** Carapace with 4 large dorsal spines posterior to orbit. (Often associated with sea anemones) ..... ***Lebbeus grandimanus*** **(Brazhnikov)**
Bering Sea to Sea of Japan and Puget Sound, Washington, 6–180 m (Butler 1980, Wicksten and Mendez 1982).

Carapace with 1–2 dorsal spines posterior to orbit. (Associations various or not known) ..... **25**

**25** Dactyl of third pereopod simple, without spines ..... ***Lebbeus scrippsi*** **Wicksten and Mendez**
Southern Peru to off Arica, Chile, 768–1164 m (Wicksten and Mendez 1982).

Dactyl of third pereopod with spines ..... **26**

**26** First segment of antennular peduncle with 2 anteroexternal spines. Rostrum with 5–9 ventral spines ..... ***Lebbeus splendidus*** **Wicksten and Mendez**
Off Lobos de Tierra, Peru, 712–1100 m (Wicksten and Mendez 1982).

First segment of antennular peduncle with 1 anteroexternal spine. Rostrum with 4 or less ventral spines ..... **27**

**27** Rostrum overreaching antennular peduncle, with 3–4 ventral spines ..... ***Lebbeus polaris*** **(Sabine)**
Arctic to Sea of Okhotsk, Cape Cod and northern Europe, Aleutian Islands to Alice Arm, British Columbia, 0–930 m (Green and Butler 1988).

Rostrum barely reaching end to first segment of antennular peduncle, with 1–no ventral spines ..... ***Lebbeus brandti*** **(Brazhnikov)**
Japan and Sea of Okhotsk to Wilson Bay, Alaska, 10–172 m (Wicksten and Mendez 1982).

**28 (23)** Epipods on first to fourth pereopods ..... ***Lebbeus carinatus*** **Zarenkov**
Off Peru and Chile, 1860 m (Zarenkov 1976).

Epipods on first to third pereopods ..... **29**

**29** Pleura of first to fifth abdominal segments ending in 1–3 spines. Four large spines on dorsal midline of carapace ..... ***Lebbeus groenlandicus*** **(Fabricius)**
Arctic to Cape Cod, Sea of Okhotsk, Puget Sound, 11–518 m (Butler 1980).

Pleura of at least first to third abdominal segments pointed to rounded, but not ending in 1–3 spines. One to 3 spines on dorsal midline of carapace ..... **30**

**30** Rostrum reduced to spine on frontal margin of carapace. Three spines on anterior dorsal midline of carapace ..... **31**

Rostrum prominent, not reduced to spine. 1–2 spines on anterior dorsal midline of carapace..... **32**

**31** Telson with 2 pair dorsal pines. No large, decurved spines below articular knobs of posterolateral margin of fourth and fifth abdominal somites..... ***Lebbeus catalepsis*** **Jensen**
Strait of Juan de Fuca, low intertidal zone (Jensen 1987).

Telson with 3 pair dorsal spines. Large, decurved spines present below articular knobs of posterolateral margin of fourth and fifth abdominal somites ..... ***Lebbeus lagunae*** **(Schmitt)**
Pacific Grove, California to Cedros Island, Baja California, 0–74 m (Wicksten 1978, 1988).

**32** Antennular peduncle extending to near middle of scaphocerite. Small subtidal species ..... **33**

Antennular peduncle extending nearly to end of scaphocerite. Large species of continental slopes ... **35**

**33** Dorsal surface of second abdominal segment without transverse furrow and fold. Rostrum not overreaching eye ..... ***Lebbeus zebra*** **(Leim)**
East coast of Canada, Bering Sea, Kamchatka, British Columbia, off Santa Rosa Island, California, subtidal–140 m (Wicksten and Mendez 1982).

Dorsal surface of second abdominal segment with transverse furrow and fold. Rostrum overreaching eye ..... **34**

**34** Rostrum short, not reaching end of first segment of antennular peduncle, with 2–5 dorsal spines and 1 ventral spine ..... ***Lebbeus schrencki*** **(Brazhnikov)**
Pribilof Islands to Sea of Japan to Passage Island, Strait of Georgia; 12–183 m (Butler 1980, Jensen and Armstrong 1987).

Rostrum reaching end of scaphocerite, with 5–7 dorsal spines and 3–4 ventral spines ..... ..... ***Lebbeus possjeticus*** **Kobyakova**
Possjet Bay, USSR, Bering Island and off San Nicolas Island, California; 3–57 m (Wicksten and Mendez 1982).

**35** First segment of antennular peduncle with 1 spine, bi- or trifurcated. Northern hemisphere ... ..... ***Lebbeus washingtonianus*** **(Rathbun)**
Anthony Island, Queen Charlotte Islands to off San Clemente Island, California; 820–1808 m (Butler 1980).

First segment of antennular peduncle with 3 spines. Southern hemisphere ..... ..... ***Lebbeus bidentatus*** **Zarenkov**
Peru and Chile, 1680 m (Zarenkov 1976).

**36 (20)** Third maxilliped with exopod ..... **37**

Third maxilliped without exopod ..... **47**

**37** No epipod on any pereopod ..... **38**

Epipod on at least on first pereopod..... **40**

**38** Rostrum deep, shorter than carapace, eyes large ..... ***Eualus macrophthalmus*** **(Rathbun)**
Unalaska to Point Sur, California, 110–1163 m (Butler 1980).

Rostrum slender, as long as or longer than carapace, eyes smaller ..... **39**

**39** Posterior margin of third to sixth abdominal segments armed with median dorsal spine .....
..... ***Eualus barbatus*** **(Rathbun)**
Pribilof Islands to Santa Monica Bay, California, 82–507 m (Butler 1980, Wicksten 1984).

Posterior margin of third to sixth abdominal segments unarmed ..... ***Eualus biunguis*** **(Rathbun)**
Bering Sea to Sea of Japan and Oregon, 90–2090 m (Butler 1980).

**40 (37)** Epipods on all 3 pereopods ..... **41**

Epipods on first and sometimes second pereopods ..... **45**

**41** Rostrum with dorsal margin markedly convex over eye, 7–14 spines ..... ***Eualus avinus*** **(Rathbun)**
Pribilof Islands to Oregon, 46–642 m (Butler 1980).

Rostrum nearly straight over eye, fewer (2–9) spines ..... **42**

**42** Rostrum not reaching second segment of antennular peduncle ..... **43**

Rostrum reaching second segment of antennular peduncle ..... **44**

**43** Rostrum with 2–5 dorsal teeth, telson with 3–4 pair dorsolateral spines. First pereopod slender, merus about 5× as long as wide ..... ***Eualus pusiolus*** **(Krøyer)**
Bering Sea to British Columbia and Sea of Japan, Gulf of St. Lawrence to Cape Cod, northern Europe to Spain, 0–1381 m (Butler 1980).

Rostrum with 1–3 dorsal teeth, telson with 3 pair dorsolateral spines. First pereopod stout, merus about 1.6× as long as wide ..... ***Eualus dozei*** **(A. Milne-Edwards)**
Chile-Cape Horn, 13–300 m (Holthuis 1952).

**44** Pleuron of fourth abdominal segment with ventral spine ..... ***Eualus lineatus*** **Wicksten and Butler**
Sitka, Alaska to Gulf of California, 18–232 m (Wicksten and Butler 1983, Wicksten 1988).[8]

Pleuron of fourth abdominal segment without spine ..... ***Eualus berkeleyorum*** **Butler**
Pribilof Islands to off Trinidad Harbor, California, 46–384 m (Butler 1980, Wicksten 1984, Jensen and Armstrong 1987).

**45 (40)** Normal size epipods on first and second pereopods ..... ***Eualus townsendi*** **(Rathbun)**
Pribilof Islands to Sea of Japan and Puget Sound, 38–630 m (Butler 1980).

Normal or reduced epipods on first pereopods, second pereopods with reduced epipods if present .... **46**

**46** Most of distal part of rostrum lacking spines on dorsal margin ..... ***Eualus fabricii*** **(Krøyer)**
Bering Sea to Sea of Japan and British Columbia, northwest Atlantic Ocean south to Massachusetts Bay, 4–255 m (Butler 1980).

Distal half of rostrum with dorsal spines ..... ***Eualus suckleyi*** **(Stimpson)**
Bering Sea to Sea of Okhotsk and Grays Harbor, Washington, 11–1025 m (Butler 1980).

**47 (36)** Ventral margin of fourth pleuron without spine ..... **48**

Ventral margin of fourth pleuron with spine ..... **59**

**48** Epipod absent on third maxilliped ..... ***Heptacarpus tenuissimus*** **Holmes**
Bird Island, Alaska to Santa Catalina Island, California, 2–137 m (Butler 1980).[9]

Epipod present on third maxilliped ..... **49**

**49** Epipods present on first and second or first to third pereopods ..... **50**

Epipods absent from all pereopods ..... **52**

**50** Epipods present on first to third pereopods ..... ***Heptacarpus carinatus*** **Holmes**
Dixon Harbor, Alaska, to Point Loma, California, 0–27 m (Butler 1980).

Epipods present on first and second pereopods ..... **51**

**51** Posterior margin of third abdominal segment produced, forming rounded carina. Rostrum at least as long as carapace, with 5–8 ventral teeth ..... ***Heptacarpus flexus*** **Rathbun**
Bering Sea to Farallon Islands, California, 37–172 m (Schmitt 1921).[10]

Posterior margin of third abdominal segment not produced. Rostrum shorter, not reaching end of scaphocerite, with 1 ventral tooth ..... ***Heptacarpus herdmani*** **(Walker)**
"Puget Sound" (Wicksten and Butler 1983).

**52 (49)** Pterygostomian spine absent ..... **53**

Pterygostomian spine present ..... **55**

**53** Rostrum shorter than carapace, distal ventral half convex .... ***Heptacarpus brachydactylus*** **(Rathbun)**
Monterey Bay to off Santa Cruz Island, California, 486–763 m (Standing 1981).

Rostrum longer than carapace, distal ventral half not convex or only slightly so ..... **54**

**54** Rostrum overreaching scaphocerite, without dorsal teeth on distal half .....
..... ***Heptacarpus stylus*** **(Stimpson)**
Chichagof Island, Alaska to Puget Sound, 0–439 m (Butler 1980).

Rostrum barely exceeding scaphocerite, with dorsal teeth on distal half .....
..... ***Heptacarpus franciscanus*** **(Schmitt)**
San Francisco Bay, California, to Todos Santos Bay, Baja California, 5–14 m (Schmitt 1921, Carvacho and Olson 1984).

**55 (52)** Rostrum with tiny lateral spinule on each side, located laterally near base .....
..... ***Heptacarpus yaldwyni*** **Wicksten**
Off Salina Cruz, Mexico, 1052–1145 m (Wicksten 1984).

Rostrum without tiny lateral spinule on each side ..... **56**

**56** Scaphocerite shorter than carapace; sixth abdominal somite longer than telson .....
..... ***Heptacarpus decorus*** **(Rathbun)**
Gabriola Island, Strait of Georgia to San Diego, California, 22–313 m (Butler 1980).

Scaphocerite as long as or longer than carapace; sixth abdominal somite shorter than telson ..... **57**

**57** Three spines on carapace and rostrum; none anterior to eye ..... ***Heptacarpus tridens*** **(Rathbun)**
Aleutian Islands to Cape Flattery, Washington, 0–110 m (Butler 1980).

Five to six spines on carapace and rostrum, extending anterior to eye ..... **58**

**58** Dorsal posterior margin of third abdominal somite prominent; third maxilliped extending to middle of scaphocerite ..... ***Heptacarpus camtschaticus*** **(Stimpson)**
Bering Sea to Tokyo Bay and Strait of Georgia, 0–108 m (Butler 1980).

Dorsal posterior margin of third abdominal somite flattened, third maxilliped extending almost to end of scaphocerite ..... ***Heptacarpus kincaidi*** **(Rathbun)**
East coast of Vancouver Island to San Pedro, California, 10–183 m (Butler 1980).

**59 (47)** Epipod only on first pereopod ..... **60**

Epipods on first and second, or first to third pereopods ..... **62**

**60** Pterygostomian spine absent ..... ***Heptacarpus littoralis*** **Butler**
Baranof Island, Alaska to Seattle, Washington, 0–18 m (Butler 1980, Jensen and Armstrong 1987).

Pterygostomian spine present ..... **61**

**61** Outer antennular flagellum extending beyond scaphocerite by about half length of former; lower limb of rostrum broader than upper ..... ***Heptacarpus moseri*** **(Rathbun)**
Bering Sea to Destruction Island, Washington; 0–1100 m (Butler 1980).

Outer antennular flagellum barely extending beyond scaphocerite; lower limb of rostrum scarcely broader than upper ..... ***Heptacarpus sitchensis*** **(Brandt)**
Resurrection Bay, Alaska, to Yaquina Bay, Oregon, 0–12 m (Butler 1980).

**62 (59)** Epipods on first and second pereopods ..... **63**

Epipods on first to third pereopods ..... **65**

**63** Rostrum barely reaching end of first segment of antennular peduncle .....
..... ***Heptacarpus pugettensis*** **Jensen**
Seattle, Washington to near Morro Bay, California, intertidal (Jensen 1983, Wicksten 1988).

Rostrum exceeding end of first segment of antennular peduncle, reaching to end of entire antennular peduncle or beyond ..... **64**

**64** Rostrum usually reaching to end of scaphocerite but at least to base of antennular flagellum, ventral teeth of rostrum widely spaced ..... ***Heptacarpus paludicola*** **Holmes**
Tava Island, Alaska, to San Diego, California, 0–10 m (Butler 1980).

Rostrum reaching end of or barely exceeding antennular peduncle, ventral teeth of rostrum crowded
..... ***Heptacarpus pictus*** **(Stimpson)**
San Francisco Bay, California, to off Thurloe Head, Baja California, 0–19 m (Wicksten 1988).

**65 (62)** Dactyls of pereopods 3–5 simple and falcate, rostrum slightly ascending over eye and with dorsal teeth most thickly set in proximal half ..... ***Heptacarpus stimpsoni*** **Holthuis**
Sheep Bay, Alaska, to WSW of Punta Abreojos, Baja California, 0–73 m (Butler 1980, Wicksten 1988).[11]

Dactyls of pereopods 3–5 bifid and with small spines on flexor margin, rostrum not slightly ascending over eye and with dorsal teeth more widely spaced ..... **66**

**66** Rostrum not reaching as far as cornea of eye, with series of teeth angled downward from anterior margin of carapace to tip ..... ***Heptacarpus taylori*** **(Stimpson)**
Queen Charlotte Sound, British Columbia, to Magdalena Bay, Baja California, 0–13 m (Green and Butler 1988).

Rostrum exceeding cornea of eye, rostral teeth more widely spaced and not as clearly angled downward ..... **67**

**67** Spine on distal ventral flexor margin of merus of first pereopod .....
..... ***Heptacarpus fuscimaculatus*** **Wicksten**
Santa Rosa Island, California, to Guadalupe Island, Mexico, 0–295 m (Wicksten 1986, 1988).

No spine on distal ventral flexor margin of merus of first pereopod ..... **68**

**68** Rostrum usually with bifid or trifid tip, exceeding cornea, merus of third and fourth pereopods with 2 spines ..... ***Heptacarpus palpator*** **(Owen)**
Monterey Bay, California, to Isla Espiritu Santo, Gulf of California, 0–37 m (Wicksten 1986).

Rostrum usually with simple tip, not exceeding cornea, merus of third and fourth pereopods with 1 spine ..... ***Heptacarpus brevirostris*** **(Dana)**
Attu, Aleutian Islands, to Santa Cruz, California, 0–128 m (Butler 1980, Wicksten 1986).

**69 (11)** Dorsolateral antennular flagellum with accessory branch (may be free or partially fused with flagellum) ..... **70**

Dorsolateral antennular flagellum without accessory branch (may be completely fused with flagellum) ..... **72**

**70** Rostrum with 12 ventral teeth. (Rostrum with 4 dorsal teeth, 23 segments in carpus of second pereopod) ..... ***Lysmata trisetacea*** **(Heller)**
Red Sea to Hawaiian Islands, Gulf of California to Malpelo Island, 0–150 m (Wicksten 1983).

Rostrum with 1–5 ventral teeth. (Rostrum with 5–8 dorsal teeth, 17–30 segments in carpus of second pereopods) ..... **71**

**71** 17 Segments in carpus of second pereopods. Rostrum with 1 ventral tooth. In life, with white vertical stripes on abdomen ..... ***Lysmata galapagensis*** **Schmitt**
Magdalena Bay, Baja California, and Gulf of California to Galapagos Islands, 0–10 m (Wicksten 1983).

Carpus of second pereopod with 23–30 segments. Rostrum with 4–5 ventral teeth. In life, without white vertical stripes on abdomen ..... ***Lysmata intermedia*** **(Kingsley)**
Florida Keys to Tobago and Curacao, Azores, Gulf of California to Galapagos Islands and Peru (Wicksten 1983).

**72** 26–32 segments in carpus of second pereopods. Pterygostomian spine present .....
..... ***Lysmata californica*** **(Stimpson)**
Tomales Bay, California, to Panama, 0–10 m (Wicksten 1983).

21–22 segments in carpus of second pereopods. Pterygostomian spine absent .....
..... ***Lysmata porteri*** **(Rathbun)**
Chile, Juan Fernandez Islands (Holthuis 1952).[12]

## Notes

[1] Rios and Carvacho (1982) reported *L. parvulus* (Stimpson) from the Gulf of California, and stated that *L. antiborealis* could be a synonym of the former species. However, they gave no justification for the synonymy. The two species are treated here as amphipanamic sibling species.

[2] *Hippolyte mexicana* Chace, 1937 is a synonym (Wicksten 1983).

[3] *Thor algicola* is a sibling species of *T. manningi* Chace, 1972. It was misidentified as *T. paschalis* (Heller) in previous works.

[4] *Thor amboinensis* has been collected at Isla Manuelita, Cocos Island, 20 m, among coral slabs and rock, 16–25 November 1989, Alex Kerstitch, 1 ovigerous female, University of Southern California collections (USC).

[5] The southernmost record of *S. prionota* is 6.5 mi. SW of San Carlos Point, Baja California (29°33′13″N, 115°36′07″W–29°33′30″N, 115°33′38″W), 37 m, rock dredge, 25 April 1950, *Velero IV* sta. 1944–50, 2 specimens, USC.

[6] *Spirontocaris bispinosa* Holmes is a synonym of *S. holmesi* Holthuis, 1947.

[7] The southernmost record of *S. snyderi* is San Cristobal Bay, Baja California (27°24′28″N, 114°39′40″W–27°26′00″N, 114°37′30″W), 75 m, 27 April 1950, *Velero IV* sta. 1949–50, 1 specimen, USC.

[8] *Eualus lineatus* has been given the name *E. herdmani* in the past due to confusion with *Heptacarpus herdmani* (Walker) (Wicksten and Butler 1983). *Eualus subtilis* Carvacho and Olson, 1984 also is a synonym (Wicksten 1988).

[9]*Spirontocaris gracilis* (Stimpson) and *Hippolyte amabilis* Lenz are synonyms of *Heptacarpus tenuissimus* (Holthuis 1947, 1969).

[10]The southernmost record of *H. flexus* is 3.2 miles from Farallon Light (37°48′N, 122°59′W), 52 m, rock, 24 Sept. 1961, *Velero III* sta. 7422, 1 specimen, USC.

[11]The southernmost record of *H. stimpsoni* is 7 mi. WSW of Point Abreojos, Baja California (26°41′ 13″N, 113°42′01″W–26°39′48″N, 113°40′43″W), 37–44 m, 29 April 1950, *Velero IV* sta. 1053–50, 1 specimen, USC. *Spirontocaris cristata* (Stimpson) is a synonym (Holthuis 1947).

[12]The revision by Chace (1972) places *Hippolysmata* in synonymy with *Lysmata*, so the species now should be called *L. porteri*.

Note: Two additional species of hippolytids have been described from Monterey Bay, California: *Hippolyte affinis* Owen, 1839 and *H. layi* (Owen 1839, in Schmitt 1921). The former species has not been found again; the latter was reported off British Columbia by Bate (1866, in Schmitt 1921). From the illustrations, the former probably should be assigned to *Spirontocaris*, the latter probably is a species of *Heptacarpus*. The type material seems to have been lost. New specimens are needed in order to resolve the relationships of these two species.

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# Comparison of Fishes Taken By a Sportfishing Party Vessel Around Oil Platforms and Adjacent Natural Reefs Near Santa Barbara, California

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Since 1958, 29 oil platforms have been sited in the southern California Bight of which 28 still remain in place. However, with the exception of a few papers (Carlisle et al. 1964, Bascom et al. 1976, Allen and Moore 1976), little is known of the fish populations surrounding these structures, particularly those sited in water deeper than 30 m. Moreover, except for a brief reference in Carlisle et al., no scientific papers have been published on the use of southern California platforms by sport fishermen.

In the course of research on the Santa Barbara, California, party vessel sport fishery, it was noted that the platforms off Santa Barbara supported considerable sportfishing activity. Those platforms, located to the southeast of Santa Barbara in depths of 48–62 m (Fig. 1), were particularly important and were fished intensively for various rockfishes (genus *Sebastes*). When fishing a platform, the vessel pulled up to within 5–10 m of a platform and drifts along one side, with the vessel operator using intermittent power to keep it near the structure. Most of the desirable species, particularly rockfishes, remained close to the platforms, rarely venturing more than perhaps 20 m from the structure. The party vessels also spent considerable time fishing over nearby natural reefs. In this survey, it was noted that there appeared to be differences in species catch composition and fish size between oil platforms and these natural reefs.

Increased offshore oil drilling off California has raised interest in the role platforms play in marine systems. Questions have been raised regarding what fish live around platforms, how these structures influence populations over surrounding reefs, and whether the platforms act as fish enhancers (promoting recruitment) or only as aggregators. These questions are particularly relevant when the platforms are to be decommissioned and the possibility of allowing them to remain as artificial reefs is raised. This paper describes the results of our study on the fish populations around oil platforms and nearby natural reefs off Santa Barbara.

## Methods

The study was conducted aboard the 16-m sportfishing vessel *Hornet*, berthed in Santa Barbara. During the course of this study the *Hornet* operated 6 days per week; 3 three-quarter day trips (7 am–3 pm) and 3 half-day trips (7 am–noon, 12:30 pm–5:30 pm). The *Hornet* carried a maximum of 40 passengers. Fish taken aboard the *Hornet* were sampled weekly from April 1975 to April 1978. All fish landed were measured, even those returned alive to the water as undesirable or in compliance with bag or size-limit regulations. Each was placed on a plastic measuring sheet and the length marked. Total length was recorded to the nearest mm for all fish except members of the jack (Carangidae) and mackerel (Scombridae) families, for which fork length was taken to the nearest mm. Also recorded were the number of anglers aboard the vessel, hours fished, and the location and depth of fishing effort. Of particular importance was the total time the *Hornet* fished around or over all the fishing sites. This information was obtained through biweekly interviews with *Hornet* operators throughout the 3-year survey.

Data from this study could not give an unbiased estimate of species composition. Most angling involved fishing with live bait (primarily northern anchovies *Engraulis mordax*) or with lures simulating fishes or small crustaceans at the three sites used in this study. Thus, because the sample was biased toward relatively large-mouthed, piscivorous species, we determined distributional patterns of whatever species were taken by these methods, rather than describing entire fish communities.

For this report we have divided the study sites into three locations (Fig. 1): 4 Mile Reef, 6 Mile Reef, and five platforms. Twenty-one other reefs and kelp beds located well away from this area are not included. The 4 Mile Reef is an aggregation of 1–7 m high pinnacles in 40–50 m of water. The oil platforms fished included Platforms A, B, Hillhouse, Houchin, and Hogan. These are steel structures 25–45 m on the side, situated in water depths between 54 and 62 m. The 6 Mile Reef

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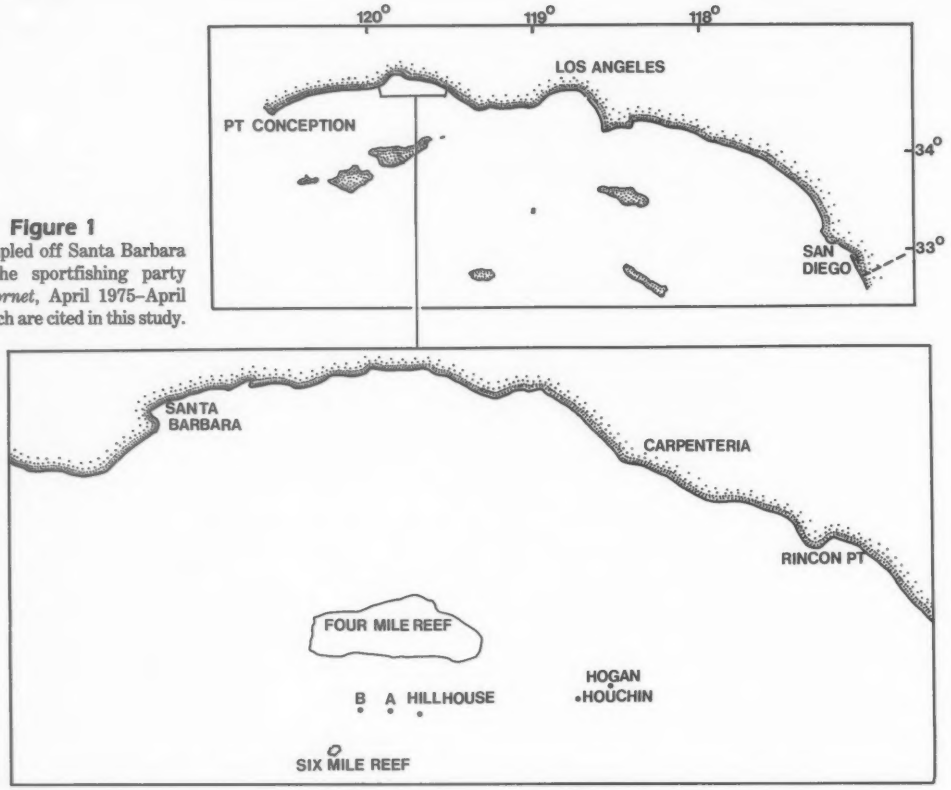



**Figure 1**
Sites sampled off Santa Barbara aboard the sportfishing party vessel *Hornet*, April 1975–April 1978, which are cited in this study.

is located in a depth of 74 m and rises to about 6 m above the substrata.

## Results

The *Hornet* spent 18.2% of its total fishing time around the platforms, compared with 18.4% over the 4 Mile Reef and 2.4% over the 6 Mile Reef (Table 1). About 17% of all fish recorded at all 24 sites were taken around the platforms, compared with 27.6% over 4 Mile Reef and 3.2% over 6 Mile Reef (Table 2).

Twenty-eight species were taken around the platforms, compared with 34 and 17 species over the 4 Mile and 6 Mile Reefs, respectively (Table 3). Rockfishes (*Sebastes* sp.) predominated the catches at all sites in both species numbers and abundance. Of all species captured at the platforms, 53.6% were rockfishes, compared with 50% at the 4 Mile Reef and 82.4% at the 6 Mile Reef. Of all fish taken around the platform, 83% were rockfishes, compare with 96.0% and 90.8% at the 6 Mile and 4 Mile Reefs, respectively. Catch-per-unit-

**Table 1**
Percent of total fishing time spent off Santa Barbara at oil platforms, 4 Mile Reef, and 6 Mile Reef, April 1975–April 1978, by the sportfishing party vessel *Hornet*. Based on biweekly interviews with *Hornet* operators.

| Site | Hours | % Total |
|---|---|---|
| 4 Mile Reef | 613.2 | 18.4 |
| Platforms | 607.6 | 18.2 |
| 6 Mile Reef | 78.5 | 2.4 |
| Other (21) sites | 2039.6 | 61.0 |

**Table 2**
Percentage, by average, of all fish sampled off Santa Barbara aboard the sportfishing party vessel *Hornet*, April 1975–April 1978.

| Site | *N* | % Total |
|---|---|---|
| 4 Mile Reef | 4 390 | 27.6 |
| Platforms | 2 746 | 17.3 |
| 6 Mile Reef | 510 | 3.2 |
| All Other Areas | 8 272 | 52.0 |

**Table 3**

All fish surveyed off Santa Barbara aboard the sportfishing party vessel *Hornet*, April 1975–April 1978, around the oil platforms (A, B, Hillhouse, Houchin, and Hogan), 4 Mile Reef, and 6 Mile Reef.

| Species | Total length (mm) | SD | *N* | % Total |
|---|---|---|---|---|
| **Oil platforms[1]** | | | | |
| *Sebastes serranoides* | 270.0 | 28.1 | 831 | 30.3 |
| *Sebastes entomelas* | 265.4 | 25.8 | 420 | 15.3 |
| *Scomber japonicus* | 358.3 | 44.8 | 283 | 10.3 |
| *Sebastes pinniger* | 238.8 | 24.3 | 191 | 7.0 |
| *Sebastes auriculatus* | 269.1 | 49.9 | 183 | 6.7 |
| *Sebastes paucispinis* | 260.8 | 32.8 | 147 | 5.4 |
| *Sebastes miniatus* | 262.1 | 37.8 | 143 | 5.2 |
| *Sebastes mystinus* | 243.0 | 27.2 | 128 | 4.7 |
| *Paralabrax clathratus* | 318.5 | 61.2 | 92 | 3.4 |
| *Sebastes hopkinsi* | 213.2 | 16.8 | 60 | 2.2 |
| *Sebastes caurinus* | 260.2 | 34.4 | 60 | 2.2 |
| *Sebastes flavidus* | 255.9 | 23.0 | 59 | 2.2 |
| *Ophiodon elongatus* | 490.2 | 136.2 | 17 | 0.6 |
| *Genyonemus lineatus* | 294.6 | 33.9 | 16 | 0.6 |
| *Trachurus symmetricus* | 226.5 | 33.1 | 15 | 0.6 |
| *Sebastes dalli* | 157.1 | 27.0 | 14 | 0.5 |
| *Medialuna californiensis* | 259.2 | 12.5 | 13 | 0.5 |
| *Paralabrax nebulifer* | 455.2 | 65.3 | 12 | 0.4 |
| *Sebastes rubrivinctus* | 238.7 | 24.7 | 12 | 0.4 |
| *Sebastes rosaceus* | 213.4 | 17.7 | 10 | 0.4 |
| *Sebastes constellatus* | 280.0 | 39.3 | 5 | 0.2 |
| *Sarda chiliensis* | 512.5 | 15.8 | 4 | 0.2 |
| *Citharichthys sordidus* | 208.7 | 11.0 | 3 | 0.1 |
| *Chromis punctipinnis* | 290.0 | 1.4 | 2 | 0.1 |
| *Scorpaena guttata* | 219.0 | 96.2 | 2 | 0.1 |
| *Scorpaenichthys marmoratus* | 362.5 | 14.8 | 2 | 0.1 |
| *Squalus acanthias* | 989.5 | 4.9 | 2 | 0.1 |
| *Sebastes umbrosus* | 147.0 | 94.8 | 2 | 0.1 |
| Total | | | 2728 | |

| Species | Total length (mm) | SD | *N* | % Total |
|---|---|---|---|---|
| **4 Mile Reef[2]** | | | | |
| *Sebastes mystinus* | 259.6 | 35.6 | 1044 | 23.8 |
| *Sebastes hopkinsi* | 215.5 | 17.1 | 947 | 21.6 |
| *Sebastes serranoides* | 294.3 | 40.1 | 750 | 17.1 |
| *Sebastes paucispinis* | 298.2 | 58.4 | 716 | 16.3 |
| *Scomber japonicus* | 306.6 | 25.8 | 228 | 5.2 |
| *Sebastes entomelas* | 189.3 | 24.4 | 97 | 2.2 |
| *Sebastes rosaceus* | 197.2 | 23.7 | 97 | 2.2 |
| *Sebastes constellatus* | 287.6 | 44.6 | 60 | 1.4 |
| *Sebastes rubrivinctus* | 266.7 | 46.7 | 57 | 1.3 |
| *Paralabrax clathratus* | 334.4 | 85.9 | 54 | 1.2 |
| *Sebastes auriculatus* | 333.4 | 67.6 | 51 | 1.2 |
| *Sebastes miniatus* | 375.5 | 90.6 | 42 | 1.0 |
| *Ophiodon elongatus* | 537.3 | 117.9 | 36 | 0.8 |
| *Sebastes umbrosus* | 197.7 | 28.1 | 30 | 0.7 |
| *Sebastes caurinus* | 346.7 | 57.6 | 25 | 0.6 |
| *Sebastes dalli* | 136.9 | 27.9 | 16 | 0.4 |
| *Anoplopoma fimbria* | 216.9 | 2.0 | 14 | 0.3 |
| *Atractoscion nobilis* | 378.6 | 166.0 | 12 | 0.3 |
| *Chromis punctipinnis* | 310.6 | 48.4 | 10 | 0.2 |
| *Genyonemus lineatus* | 303.2 | 52.1 | 10 | 0.2 |
| *Sebastes pinniger* | 241.8 | 98.3 | 10 | 0.2 |
| *Trachurus symmetricus* | 272.8 | 20.7 | 9 | 0.2 |
| *Scorpaena guttata* | 253.6 | 43.5 | 7 | 0.2 |
| *Sebastes flavidus* | 255.3 | 33.1 | 7 | 0.2 |
| *Semicossyphus pulcher* | 545.8 | 69.0 | 5 | 0.1 |
| *Paralabrax nebulifer* | 531.8 | 61.7 | 5 | 0.1 |
| *Sebastes carnatus* | 218.3 | 13.3 | 4 | 0.1 |
| *Hydrolagus colliei* | 500.3 | 81.3 | 3 | 0.1 |
| *Medialuna californiensis* | 250.0 | 12.7 | 2 | <0.1 |
| *Sarda chiliensis* | 440.5 | 7.8 | 2 | <0.1 |
| *Squatina californica* | 1040.5 | 57.3 | 2 | <0.1 |
| *Eptatretus stouti* | 287.0 | 0.0 | 1 | <0.1 |
| *Synodus lucioceps* | 328.0 | 0.0 | 1 | <0.1 |
| Total | | | 4354 | |

| Species | Total length (mm) | SD | *N* | % Total |
|---|---|---|---|---|
| **6 Mile Reef[3]** | | | | |
| *Sebastes mystinus* | 262.5 | 42.3 | 146 | 28.6 |
| *Sebastes entomelas* | 309.7 | 28.0 | 112 | 22 |
| *Sebastes hopkinsi* | 234.0 | 27.0 | 85 | 16.7 |
| *Sebastes pauscispinis* | 307.6 | 60.7 | 75 | 14.7 |
| *Sebastes rubrivinctus* | 270.8 | 43.8 | 26 | 5.1 |
| *Sebastes serranoides* | 286.6 | 47.5 | 20 | 3.9 |
| *Genyonemus lineatus* | 301.6 | 21.7 | 17 | 3.3 |
| *Sebastes constellatus* | 267.4 | 70.9 | 5 | 1.0 |
| *Sebastes miniatus* | 387.6 | 57.3 | 5 | 1.0 |

| Species | Total length (mm) | SD | *N* | % Total |
|---|---|---|---|---|
| *Sebastes chlorostictus* | 205.3 | 22.1 | 4 | 0.8 |
| *Sebastes caurinus* | 357.0 | 58.2 | 3 | 0.6 |
| *Ophiodon elongatus* | 639.0 | 172.5 | 2 | 0.4 |
| *Sebastes flavidus* | 297.5 | 0.7 | 2 | 0.4 |
| *Paralabrax nebulifer* | 537.0 | 0.0 | 1 | 0.2 |
| *Sebastes dalli* | 157.0 | 0.0 | 1 | 0.2 |
| *Sebastes rosaceus* | 171.0 | 0.0 | 1 | 0.2 |
| *Sebastes umbrosus* | 186.0 | 0.0 | 1 | 0.2 |
| Total | | | 506 | |

[1]No. trips = 15; No. anglers = 352; No. hours fished = 47.0; Effort = 8251 angler hours; CPUE = 0.33 fish per angler hour; $H' = 1.03$.

[2]No. trips = 24; No. anglers = 454; No. hours fished = 79.8; Effort = 36 206 angler hours; CPUE = 0.12 fish per angler hour; $H' = 0.95$.

[3]No. trips = 6; No. anglers = 58; No. hours fished = 12.5; Effort = 725 angler hours; CPUE = 0.70 fish per angler hour; $H' = 0.95$.

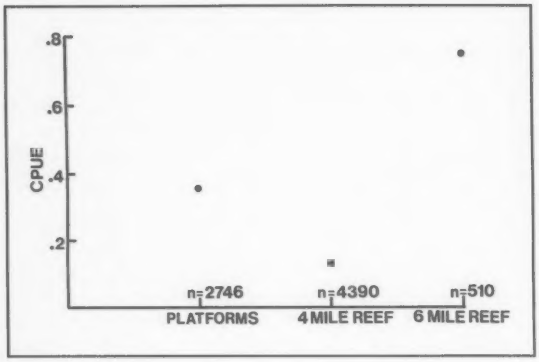
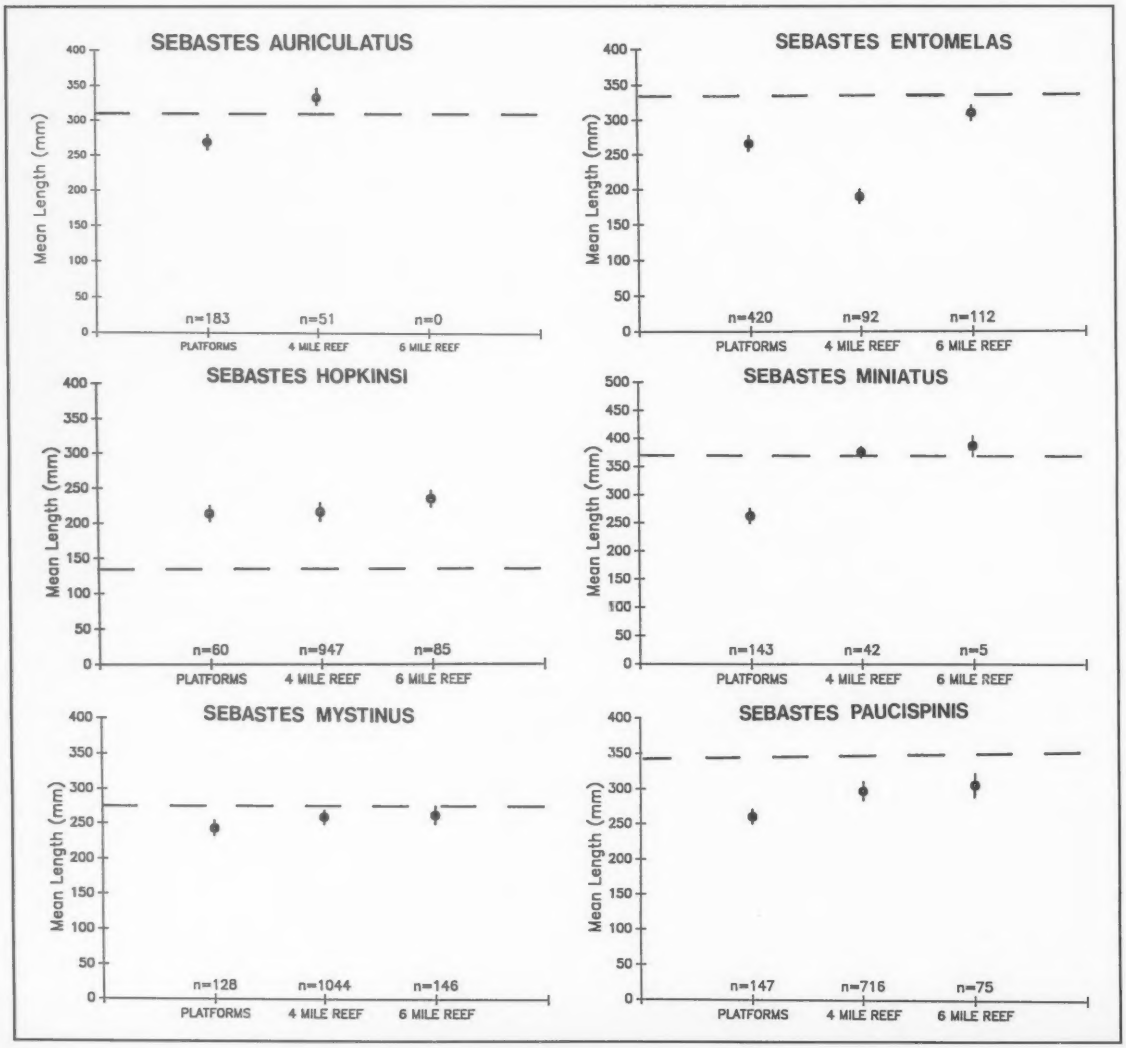



**Figure 2**
Catch-per-unit-effort (number of fish taken per angler hour) of all species caught aboard the sportfishing vessel *Hornet*, based on sampling during April 1975–April 1978 at three sites off Santa Barbara.

**Table 4**
Kendall tau rank correlation analysis of the top ten species taken by the sportfishing party vessel *Hornet*, April 1975–April 1978, at three sites off Santa Barbara, California.

| | | |
|---|---|---|
| 6 Mile Reef | $\tau$ = 0.13 | |
| | $p$ = 0.26 | |
| | $N$ = 14 | |
| 4 Mile Reef | $\tau$ = 0.00 | $\tau$ = 0.72 |
| | $p$ = 0.50 | $p$ = 0.01 |
| | $N$ = 14 | $N$ = 14 |
| | Platform | 6 Mile Reef |



effort (CPUE), defined as number of fish taken per angler hour, was highest at the 6 Mile Reef, followed by the platforms and the 4 Mile Reef (Fig. 2).

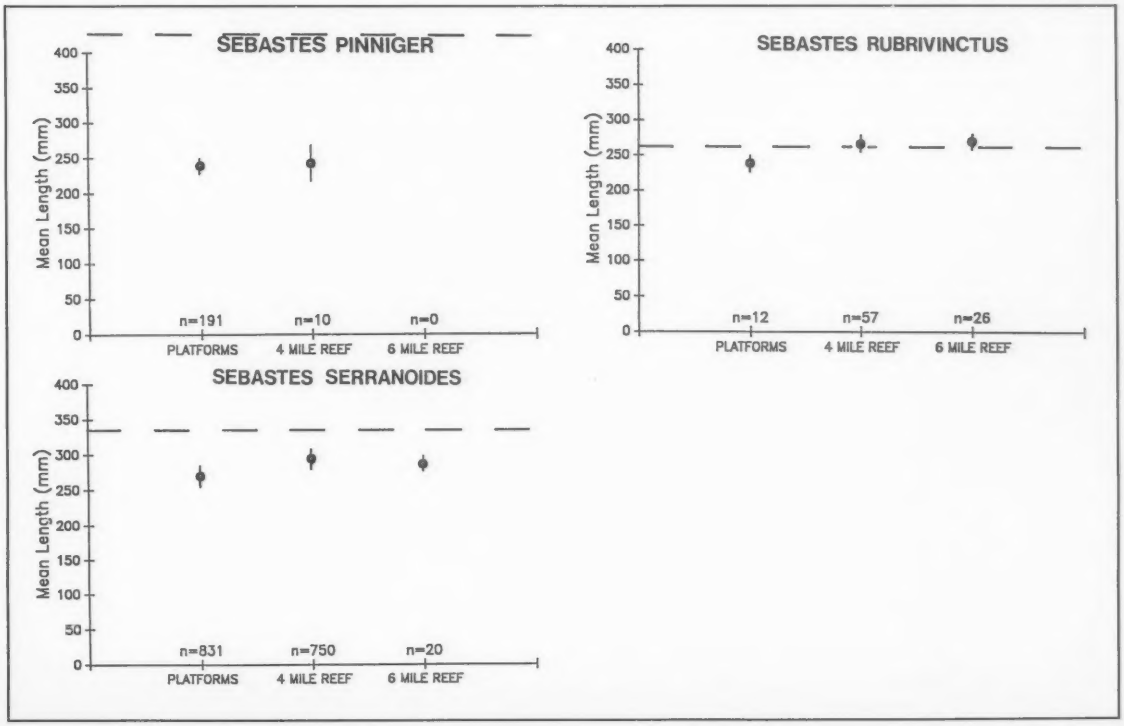
At the platforms (Table 3) rockfish made up 8 of the 10 most-frequently-taken species. While olive rockfish *Sebastes serranoides*, widow rockfish *S. entmelas*, chub mackerel *Scomber japonicus* comprised 55.9% of the total catch, a number of other species (including canary rockfish, *Sebastes pinniger*, brown rockfish *S. auriculatus*, and bocaccio *S. paucispinis* were also taken in some numbers. AT the 4 Mule Reef, 8 of the top 10 species were rockfish, with blue rockfish *Sebastes mystinus*, squarespot rockfish *S. hopkinsi*, *S. serranoides*, and *S. paucispinis* dominating the catch, making up 78.8%. Nine of the top 10 species at the 6 Mile Reef were rockfish and *S. mystinus*, *S. entomelas*, *S. hopkinsi*, and *S. paucispinis* were taken in the largest numbers, forming 82.0% of the total.

We compared the rank abundances of the top 10 species at the three sites with the Kendal tau coefficient test (Sokal and Rohlf 1969). Based on this measure, species composition was significantly correlated between natural reefs only, and species arrays from natural reefs were not correlated with that of the platform (Table 4). The primary differences between the reefs and platforms were the relative abundances of *S. hopkinsi*, *S. mystinus*, starry rockfish *S. constellatus*, and flag rockfish *S. rubrivinctus* at the natural reefs and the scarcity of *S. auriculatus* and *S. pinniger* over these reefs.

With only a few exceptions, all rockfish taken around the platforms were juveniles (Fig. 3). A major exception was *S. hopkinsi*, a species in which all individuals takn were mature. In addition, a few adult *S. auriculatus* and *S. mystinus* were caught, as well as one vermillion rockfish *S. miniatus*. At the 4 Mile Reef, a higher percentage of fish were mature. Again, all *S. hopkinsi* taken were adults, as were most *S. auriculatus* and *S. miniatus*, many *S. mystinus* and *S. rubrivinctus*, and a few *S. serranoides*. In general, more adult rockfish were taken over the 6 Mile Reef than at the other two stations. All *S. hopkinsi* were mature,

**Figure 3 (bottom facing page and below)**

Mean size (with 95% confidence interval) of 9 species caught aboard the sportfishing party vessel *Hornet*, based on sampling during April 1975–April 1978 at three sites off Santa Barbara. Also included are 50% lengths at maturity from data in Wyllie Echeverria (1987), Love et al. (1990), and Love (unpubl. data).



as were most *S. miniatus* and *S. rubrivinctus* and many *S. entomelas*, *S. mystinus*, *S. paucispinis*, and *S. serranoides*.

## Discussion

During the period sampled, the platforms were important sites for the *Hornet*'s fishing effort. They were also fished by other sportfishing party vessels from Ventura Harbor, about 30 km to the east, though we are unsure of the total effort from these vessels. In both circumstances, these structures provided the vessel operators with a relatively reliable source of easily caught, though generally small, fish. The ease with which small rockfish were caught made the platforms particularly attractive to the *Hornet*'s operators on half-day runs, when the vessels carried many inexperienced fishermen. The platforms were also utilized when fishing was poor at other locations for more desirable species, such as kelp bass *Paralabrax clathratus*.

We have recently (1989) discussed platform fishing with current Santa Barbara party vessel operators. They report that though the platforms are still fished for small rockfish, kelp bass are an equal or more important species during summer months. This is particularly true of the eastern platforms, particularly Houchin, Hogan, and Hope (2 km east of Hogan). Though there are five platforms in this complex, only these three are routinely fished. During the season's peak, as many as 300–400 *P. clathratus* per trip are caught from around a single platform. Based on tagging studies by P. Hart (Dep. Biol. Sci., Univ. Calif., Santa Barbara 93106, pers. commun., Sept. 1988), it is likely that kelp bass move onto the platforms before summer and leave in the fall, traveling both east and west, with reported movements of as much as 32 km in 6 months.

In the study conducted between 1975 and 1978, there were significant differences in both species compositions and mean sizes between the three sites (though the natural reefs were much more similar with each other). Much of the differences in species composition between the platforms and the natural reefs came from the relative abundance of high-relief substrate-associated rockfish (such as *S. constellatus* and *S. rubrivinctus*) over the reefs and their near absence around the platforms. The substrata around these structures are composed of a mixture of drill cuttings and mussels which have broken off the platform pilings. This does not appear to be suitable habitat for many rockfish species.

On the other hand, a few substrate-associated species, such as juvenile *S. auriculatus* and *S. pinniger*, were most abundant around the platforms. *Sebastes auriculatus* (both juveniles and adults) are most often found associated with low relief or the sand-rock interface, habitat most similar to that around the platforms. We do not know what substrata juvenile *S. pinniger* prefer, though its abundance around the platforms and scarcity over natural reefs imply it favors habitats similar to *S. auriculatus*.

It is unclear why *S. mystinus* and particularly *S. hopkinsi* should be relatively uncommon around the platforms, yet abundant on the reefs. Both species are midwater planktivores, always found in association with high relief. A possibility is that both species take refuge in crevices at night and that these are relatively uncommon on the platform pilings and cross members.

Differences in depths between the sites were probably responsible for only a few of the observed differences in species abundances and sizes. The absence of *P. clathratus* from the 6 Mile Reef was undoubtedly due to the reef's relatively extreme depth. The 6 Mile Reef is situated in 74 m, well below the 46 m maximum depth of *P. clathratus* (Eschmeyer et al. 1983). Love et al (in review) summarizing ontogenetic *Sebastes* movements, noted that almost all species recruit to waters shallower than adult depth, subsequently moving to deeper water as they mature. If depth were a major factor in our study, we would expect to see the smallest rockfish at the shallowest (4 Mile Reef) station. However, while both large and small individuals of many rockfish species were taken at 4 Mile Reef, the mean size of most species (except for *S. entomelas*) was actually larger than at the other two sites.

Are the platforms we sampled aiding rockfish production or do they only act as aggregators? In other words, do rockfish recruit from the plankton to the platforms or do they settle out elsewhere and later migrate to these structures? Though our data is not sufficient to answer the question, there is evidence that at least some recruitment takes place around Santa Barbara platforms. In the only detailed study of a California platform, Carlisle et al. (1964) found that both *S. paucispinis* and *S. serranoides* recruited to platform Hazel, located in 30 m of water, about 6 km inshore of our study platforms. We believe it is likely that some rockfish species (i.e., *S. entomelas*, *S. mystinus*, *S. paucispinis*, *S. pinniger*, and *S. serranoides*) recruit to our platforms, particularly in light of the large numbers of small fish, most only 1–2 years old. Smaller and younger fish may be present at these platforms, but their small size precludes their being taken by hook-and-line.

There are several reasons that mature rockfish are rare around the platforms. While juveniles of deep-water species (i.e., *S. entomelas*, *S. pinniger*, *S. paucispinis*) are able to tolerate the warm shallow waters around these structures, the adults are not (Love et al.,

In review). Their subadults make ontogenetic shifts into deeper water. Secondly, fishing pressure around the platforms probably crops many larger individuals. Lastly, it is possible that artificial habitat in some unknown way discourages adult rockfish. F. Matthews (Dep. Oceans and Fish., Pacific Biol. Stn., Nanaimo, B.C., Canada V9R 5K6, pers. commun., May 1989) found that only immature rockfish occurred on an artificial reef in Puget Sound. Natural reefs supported both juveniles and adults.

As discussed before, most rockfish species (including *S. entomelas* and *S. paucispinis*) recruit to shallow water, then migrate into deeper zones as they mature. Based on catch rates, we have noted on several occasions that large aggregations of these species were present around the platforms for months, only to suddenly disappear. Hartmann (1987) tagged juvenile *S. paucispinis* around these platforms and noted recoveries from as much as 148 km away. In all cases the fish were taken in water considerably deeper than tagging depths. Thus, it is quite possible that some rockfish species settle out around these platforms, live there for a few years, and leave for deeper adult habitats, perhaps at considerable distances from the original recruitment site.

## Conclusions

Platforms were important fishing locations for the sportfishing party vessel surveyed. About 18% of its total fishing time and 17% of the total catch occurred around the platforms. This compares with about 21% of fishing time and 31% of total catch at the nearby natural reefs. Rockfish dominated the catch at both the platforms and at the natural reefs. Confirming what we had first observed, there were significant differences in catches between the platforms and natural reefs. Juvenile rockfish composed most of the platform catch, while mature rockfish were more abundant over reefs. While midwater rockfish species were abundant at both platform and natural reefs, species compositions were different, with those benthic rockfish characteristics of high-relief substrata absent or rare around the platforms.

## Acknowledgments

I thank Alfred W. Ebeling for reviewing this manuscript. Fred Benko of Sea Landing Sportfishing graciously allowed me space on the *Hornet*. I particularly thank partyboat operators Chet Phelps, Irv Grisbeck, Frank Hampton, George Kelly, and Dick Clift for making sampling possible.

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# Problems Identifying Tuna Larvae Species (Pisces: Scombridae: *Thunnus*) from the Gulf of Mexico

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The identification of tuna larvae of the genus *Thunnus* is very difficult. Five species of the genus *Thunnus* may spawn in the Gulf of Mexico: *albacares*, *obesus*, *alalunga*, *thynnus*, and *atlanticus*. Criteria for their identification have been established by Matsumoto et al. (1972), Potthoff (1974), and by Richards and Potthoff (1974). A combination of pigment patterns and osteological characters is the criteria used. Pigment patterns are used for larvae in the 3mm-NL to 10mm-SL size range, and osteological characters are used in larvae larger than 5 mm NL just during and after notochord flexion. Larvae larger than 7 mm SL are rare and pigment characters are not as useful since juvenile pigmentation begins to obscure the larval pigmentation, and larvae less than 5 mm NL usually do not have sufficient cartilage or bone development to determine vertebral counts or first closed hemal arch location. The combination of both character sets does allow for reliable identification in most cases. Clearing and staining larvae and the subsequent osteological examination are very time-consuming, whereas pigment pattern analysis is quite fast during normal larval ichthyoplankton identification. We conduct extensive ichthyoplankton surveys of the Gulf of Mexico annually (Richards et al. 1984, Kelley et al. 1986), and it is impractical to clear, stain, and perform osteological examination on all *Thunnus* obtained. In this study we cleared, stained, and osteologically examined all *Thunnus* larvae collected in 1982 (Richards et al. 1984) to determine a baseline value for species occurrence.

## Methods

A total of 362 *Thunnus* (4.5 mm NL–9.1 mm SL) larvae were examined for the presence of black pigment on the upper and lower jaw tips, along the ventral midline of the tail, along the dorsal midline, along the lateral midline, and on the caudal fin. Since these specimens had been fixed in formalin and preserved in ethanol, red pigments were no longer present. All *Thunnus* larvae taken during 1982 and a few from 1983 were utilized, except for those which were typical *T. thynnus* (possessing pigment on both the dorsal and ventral margins of the tail) or those specimens less than 4.4 mm NL. Following pigmentation examination, specimens were cleared and stained following Potthoff (1984), and vertebral counts and position of the first closed hemal arch determined. Species identification followed the criteria established by Matsumoto et al. (1972), Potthoff (1974), and by Richards and Potthoff (1974) for North Atlantic *Thunnus* species (Table 1).

## Results

Of the 362 larvae, 95 larvae will not be considered further because 4 were typical *thynnus*, 11 had no tail pigment and were too small for osteological data, 61 had ventral tail pigment and were too small for osteological data, 3 were not *Thunnus*, and 16 were lost or badly damaged during the clearing and staining process. Of the remaining 267 larvae, 241 could be reliably identified (Table 2). Most of the larvae consisted of the *atlanticus* morph with ventral tail pigment (72.7%), although a few (6.0%) lacked this. Those with ventral tail pigment are inseparable from *obesus* except by osteological criteria, and those without it are inseparable from *albacares*. Only 4.9% were *obesus*, only 6.0% were *albacares*, and 2 larvae (0.7%) were *alalunga*. The remaining 26 larvae (9.7%) cannot be positively identified (Table 3). These data demonstrate the variability which can be found in these species.

## Discussion

When Richards and Potthoff (1974) made a similar study, their specimens were mainly from the Caribbean Sea and Straits of Florida. They also found that the abundant species was *atlanticus*, with few *albacares* and *obesus* larvae confirmed in the western Atlantic. These results confirm this same

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**Table 1**
Criteria for identification of larval *Thunnus*.

| | *alalunga* | *albacares* | *atlanticus* | *obesus* | *thynnus* |
|---|---|---|---|---|---|
| Dorsal tail pigment | No | No | No | No | Yes |
| Ventral tail pigment | No | No | Yes/No | Yes | Yes |
| Lower jaw pigment | No | Yes | Yes | Yes | Yes |
| Vertebrae | 18+21 | 18+21 | 19+20 | 18+21 | 18+21 |
| First hemal arch | 10 | 11 | 11 | 11 | 10 |

**Table 2**
Characters of confirmed identifications of larval *Thunnus* (4.5 mm NL–9.1 mm SL). The characters of the remaining 26 unidentifiable larval *Thunnus* are given in Table 3.

| No. | % | Ventral tail | Dorsal tail | Vertebrae | Haemal arch | Identification |
|---|---|---|---|---|---|---|
| 194 | 72.7 | Present | Absent | 19+20 | 11 | *atlanticus* |
| 16 | 6.0 | Absent | Absent | 19+20 | 11 | *atlanticus* |
| 16 | 6.0 | Absent | Absent | 18+21 | 11 | *albacares* |
| 13 | 4.9 | Present | Absent | 18+21 | 11 | *obesus* |
| 2 | 0.7 | Absent | Absent | 18+21 | 10 | *alalunga* |
| 26 | 9.7 | See Table 3 | | | | *Thunnus* sp. |

**Table 3**
Characters of unidentifiable larval *Thunnus*.

| No. | Ventral tail | Dorsal tail | Vertebrae | Haemal arch | Possible identity |
|---|---|---|---|---|---|
| 5 | Present | Absent | 20+19 | 11 | *atlanticus* |
| 4 | Present | Absent | 18+21 | 10 | *atlanticus/obesus/thynnus* |
| 3 | Absent | Absent | 18+21 | 12 | *albacares* |
| 2 | Present | Absent | 19+21 | 11 | *atlanticus/obesus* |
| 1 | Absent | Present | 19+20 | 11 | *atlanticus/thynnus* |
| 1 | Absent | Absent | 19+20 | 10 | *alalunga/albacares/atlanticus* |
| 1 | Absent | Absent | 19+20 | 13 | *alalunga/albacares/atlanticus* |
| 1 | Present | Absent | 18+21 | 10 | *obesus/thynnus* |
| 1 | Absent | Absent | 20+19 | 11 | *albacares/atlanticus* |
| 1 | Present | Absent | 18+21 | 12 | *atlanticus/obesus* |
| 2 | Present | Present | 19+20 | 10 | *atlanticus/thynnus* |
| 2 | Present | Present | 19+20 | 12 | *atlanticus/thynnus* |
| 2 | Present | Present | 19+20 | – | *atlanticus/thynnus* |

trend for the Gulf of Mexico. Of the larvae shown in Table 2, 78.7% are definitely *atlanticus* with 10.9% *albacares* or *obesus*. The two *alalunga* were a surprise, as the adults of that species have not been taken in the Gulf of Mexico (Collette and Nauen 1983:81); but given the variability found in these larval characters, these data should not be used as unequivocal criteria for recording this species in the Gulf. We have speculated on the identity of the specimens listed in Table 3; as one can see, this speculation raises possibilities but not certainties.

*Thunnus atlanticus* is very common in the Gulf of Mexico and spawning is widespread as evidenced by larval data ( Richards et al. 1984). *Thunnus albacares* supports a developing fishery, but spawning may not be as widespread based on our 1982 data. In future studies focusing on albacares, researchers will have to use cleared and stained specimens to confirm larval abundance reliably, since about 50% of those larvae lacking ventral tail pigment may be *atlanticus* morphs or possibly even *alalunga* (Table 2). Recently, Graves et al. (1989) have shown that small juveniles 10–21 mm

TL of *T. albacares* could be distinguished electrophoretically from *T. obesus*. In the 10–12 mm TL range, some of their specimens had ventral tail pigment and some did not, but had the *albacares* electrophoretic character. The ventral or dorsal tail pigment seen in specimens this large is the juvenile pattern and not the larval pigment pattern. Distinguishing between larval and juvenile pigmentation is very difficult in these transforming sizes, and care must be taken to document the size and nature of the pigment.

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# Improved Methods for Isolation of Fish mtDNA by Ultracentrifugation and Visualization of Restriction Fragments Using Fluorochrome Dye: Results From Gulf of Mexico Clupeids

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The isolation of mitochondrial DNA (mtDNA) for studies of restriction-site polymorphisms among fish populations is achieved by either of two general methods. The methods are those of Lansman et al. (1981) which uses ultracentrifugation in cesium-chloride/ethidium-bromide gradients to separate mtDNA from nuclear DNA, and Chapman and Powers (1984) which uses low-speed centrifugations and organic extractions to precipitate mtDNA. Although the method of Chapman and Powers (1984) results in mtDNA of lesser purity, it apparently requires fewer hours to isolate mtDNA from a greater number of specimens than the method of Lansman et al. (1981), and avoids the high cost of purchasing and servicing a typical ultracentrifuge.

The technique chosen for visualization of restriction fragments depends upon the amount of mtDNA obtainable from the specimens of interest and its purity. Neither of the commonly reported techniques, such as end-labeling and ethidium-bromide staining, is specific for mtDNA. Since end-labeling is about 1000× more sensitive, a more highly purified preparation is required than for ethidium bromide. Radio-labeled hybridization probes are highly specific for mtDNA as well as very sensitive, but require many steps for preparation (Maniatis et al. 1982) and must be periodically remade. Biotinylation may provide longer-lived hybridization probes (Graves et al. 1990) but making them also requires several steps.

Here we introduce a new combination of isolation and visualization methods for mtDNA studies which incorporate attributes of some of the above techniques and which may aid investigators developing plans to begin mtDNA studies. Our approach was developed for potential use in a population study of Spanish sardine *Sardinella aurita*, as well as of other clupeids of the western Atlantic, while mindful of the need to process statistical sample sets. Incorporated in this presentation of methodology is a brief account of our initial findings on Gulf clupeids.

## Materials and methods

### Sample collection and preparation

*Sardinella aurita* and *Opisthonema oglinum* were collected aboard commercial purse seine vessels in the nearshore regions of central-west and north Florida between April and August 1989. Male and female gonads from these samples were excised fresh or semifresh and immediately stored in 10 mL of cold MSB-$Ca^{++}$ (Table 1) for up to 7 days at 4°C. The tissue was blotted dry, weighed, minced, and then homogenized in 2 to 3 volumes of cold MSB-$Ca^{++}$ by 5 strokes of a chilled 15-mL Dounce homogenizer. The homogenates were transferred to chilled 50-mL polyethylene centrifuge tubes after addition of disodium EDTA (0.2 M, pH 7.5) to a final concentration of 10 mM.

The homogenate was centrifuged at 800 × g for 10 minutes at 4°C after which the supernatant was decanted and respun. These two spins remove nuclei and cellular debris. Mitochondria were then pelleted by centrifugation at 20,000 × g for 20 minutes at 4°C. The pellet was washed with 10–20 mL of cold MSB-EDTA (Table 1) and repelleted by centrifugation for 15 minutes at 20,000 × g.

The pellets were suspended in 2 mL of cold STE (Table 1) and the mitochondrial membranes dissolved by adding 0.10 mL of 25% SDS, vortexing briefly and incubating at 37°C for 5–8 minutes. The entire lysate was then transferred to 3.0-mL Beckman polyallomer or polycarbonate centrifuge tubes containing enough cesium chloride (Sigma #C-3032) to produce a concentration of 1.1 g CsCl per mL of lysate as in Lansman et al. (1981). To this was added 0.133 mL of 0.025 M ethidium bromide. The solution was then mixed by inverting several times, and the refractive index of each tube adjusted to 1.389 at 20°C with CsCl or STE. Solution density at this $R_f$ causes the DNA to float lower in the tube than at the $R_f$ given by Lansman et al. (1981).

Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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**Table 1**
Solutions used in isolation and purification of mtDNA.

| | | | |
|---|---|---|---|
| MSB-$Ca^{++}$ | 0.21 | M | Mannitol |
| | 0.07 | M | Sucrose |
| | 0.05 | M | Tris-HCl, pH 7.5 |
| | 3.0 | mM | $CaCl_2$ |
| MSB-EDTA | 0.21 | M | Mannitol |
| | 0.07 | M | Sucrose |
| | 0.05 | M | Tris-HCl, pH 7.5 |
| | 0.01 | M | EDTA, pH 7.5 |
| TE | 10 | mM | Tris-HCl, pH 8.0 |
| STE | 10 | mM | Tris-HCl, pH 8.0 |
| | 100 | mM | NaCl |
| | 1 | mM | EDTA, pH 8.0 |
| 20 × SSC | 3.70 | M | NaCl |
| | 0.37 | M | Na citrate, adjust pH to 7.0 with 10 N NaOH, sterilize by autoclaving |
| 10 × TAE | 0.40 | M | Tris-Base |
| | 1.15% | v/v | glacial acetic acid |
| | 0.025 | M | EDTA, pH 8.0 |

## Density-gradient ultracentrifugation

The cornerstone of our isolation method is low-volume ultracentrifugation using the Beckman TL-100 Tabletop Ultracentrifuge. The short rotor radius and high available g-forces of this product serve to significantly reduce spin times over current practices. The main requirement is simply to "downsize" existing protocols to be compatible with 3-mL centrifuge tubes. Isolation of mtDNA using the TL-100 appears to be less labor-intensive as well as faster in producing highly purified mtDNA than existing techniques.

Ultracentrifugation was accomplished at approximately 200,000 × g (70,000 rpm) overnight (15–17 hours) at 4°C in a fixed-angle rotor (Beckman TLA-100.3) with six positions. Deceleration was set at 5. Following ultracentrifugation the mtDNA bands, which are visible in fluorescent light 0.5–0.7 mm below the nuclear DNA bands (Fig. 1), were withdrawn using an 18-gauge stainless-steel hypodermic needle inserted through the top of the tube to a position slightly below the mtDNA band. Withdrawn sample volume was then adjusted to 0.5 mL with STE and extracted several times with NaCl-saturated n-butanol at room temperature to remove the ethidium bromide (Lansman et al. 1981).

Following butanol extraction, the mtDNA was ethanol-precipitated using essentially the procedure of Maniatis et al. (1982). Sample molar concentrations were adjusted by dilution with 0.33 mL of cold, sterile, distilled $H_2O$. Exactly two volumes of cold ethanol were added to the solution which is briefly vortexed.

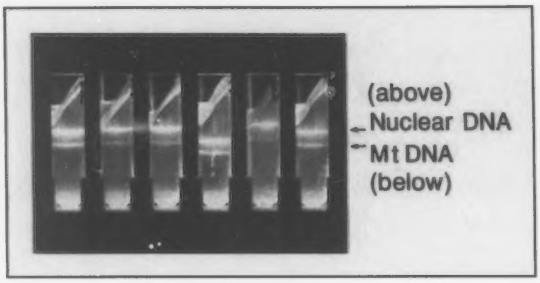


**Figure 1**
Appearance of nuclear and mitochondrial DNA bands in UV light after 17 hours of ultracentrifugation in CsCl/ethidium-bromide gradients at 200,000 × g and 4°C: upper bands are nuclear DNA, lower bands mtDNA. Material at the top of the tubes is the "skin" which forms during ultracentrifugation. Starting tissue was 1–2.5 g of ripe ovary from Spanish sardine *Sardinella aurita*.

The sample is stored overnight at −20°C after which mtDNA is pelleted by centrifugation in the fixed-angle rotor in the Beckman TL-100 at 30,000 × g for 30 minutes at 2°C. After complete drying by evaporation (no odor of ethanol remaining) the mtDNA pellet is dissolved in 50 μL of cold TE (Table 1) and stored indefinitely at −20°C.

## Fluorometric quantification of mtDNA

Yield quantification followed Paul and Myers (1982). Standard curves were generated from fluorescence of known DNA quantities in a $1.5 \times 10^{-4}$ M solution of Hoechst 33258 (CalBiochem Cat. #SR5A03-0388). Fluorescence was measured using an Aminco J4-7439 Fluoro-Colorimeter (GE F4T4/BL UV lamp and an R-136 phototube) at photomultiplier settings of 1, 3, and 10. mtDNA concentrations were calculated using the geometric mean regression of the standard curve. Yields were determined as μg mtDNA per g of starting tissue.

## Restriction endonuclease digestion

Immediately prior to digestion with restriction enzymes, samples were treated with RNAse-A to a concentration of 10 μg/mL and incubated at room temperature for 1 hour. Samples were then heated to 70°C for 5 minutes and cooled on ice before addition of the restriction enzymes. In this initial study only two six-base-pair restriction endonucleases were used: *Eco*-RI and *Hin*d-III. Digestions were carried out according to the reaction conditions specified by the manufacturers. Reaction mixtures contained 0.2–1.0 μg of mtDNA in a final volume of 20 μL adjusted with

sterile, distilled water. Using a Hamilton syringe, 2.0 μL of the digestion buffer was added to the tube and mixed by vortexing, then at least two units of the restriction enzyme were added and also mixed by vortexing. The reaction mixtures were allowed to incubate at 37°C for at least 2–3 hours, but sometimes as long as overnight. The reaction was stopped by the addition of 0.4 μL of 0.5 M EDTA (pH 7.5).

### mtDNA fragment visualization using Hoechst 33258

Restriction fragments were separated on horizontal (submerged) agarose slab gels with the Hoechst 33258 fluorochrome incorporated as described in DeFlaun and Paul (1986). The fluorochrome is a 1:30 dilution of $1.5 \times 10^{-4}$ M solution of Hoechst 33258 with 1 × SSC (i.e., 1:20 dilution of 20 × SSC, Table 1). The gel is created by boiling a 1.1% solution of agarose in distilled $H_2O$ containing 10% 10 × TAE (Table 1) buffer until clear. The suspension is allowed to cool to the touch before adding a 1.1% volume of the Hoechst 33258 dilution. After casting, the gel is allowed to set for at least 30 minutes in an opaque box to prevent photo-deactivation of the fluorochrome.

For running, the gel is immersed in a tank buffer of 500 mL distilled $H_2O$, 56 mL of 10 × TAE (Table 1), and 5.6 mL of the Hoechst 33258 dilution. Samples containing 10 μL of digested mtDNA from the reaction mixture, 1 μL of 10 × TAE, and 2 μL of tracking dye (Bromophenol blue) are then micropipetted into the wells. Outside lanes contained *Hin*d-III digested λ-DNA standards.

Gels are electrophoresed at 50 volts for approximately 3 hours, or until the tracking dye covers three-quarters of the length of the gel. The gel apparatus remains isolated from light during running. Following the run, gels were placed on a UV transilluminator and photographed with a Polaroid MP-4 Land-camera using Polaroid Type 667 black-and-white film.

### Measurement and analysis of mtDNA fragment patterns

Photographs of the gels were processed on a computer-automated optical pattern-recognition system developed by Biosonics Inc., Seattle, Washington. Fragment sizes were calculated by the global form of the reciprocal method as described by Elder and Southern (1987).

## Results

Ovarian tissue from *Sardinella aurita* and *Opisthonema oglinum* consistently produced visible mtDNA bands in the CsCl/ethidium-bromide gradient by ultracentrifugation in fewer than 17 hours (Fig. 1), but the testicular tissue did not. If carefully extracted, the mtDNA fraction was sufficiently void of contamination by RNA and nuclear DNA. With the Beckman TL-100 it is undoubtedly possible to reduce the time required for ultracentrifugation even further, since higher speeds of up to 100,000 rpm are available using polycarbonate tubes.

The only apparent drawback of the fixed-angle rotor over the swinging-bucket rotor is that in the fixed-angle rotor the cross-sectional area of the fluid in the tube is greatest while under centrifugation, but becomes less when the rotor is at rest and least when the tube is upright. Thus, the scab-like material that forms on top of the gradient during centrifugation protrudes down into the gradient when the tube is upright (Fig. 1). However, if the refractive index is adjusted carefully, both DNA bands will form below the protrusion of this scab-like material. Since this material does not crumble after centrifugation at 4°C, it can be removed or pushed aside to withdraw the mtDNA.

The mean yield of mtDNA from fresh *S. aurita* gonads stored in MSB-$Ca^{++}$ for 2 days at 4°C was $1.90 \pm 0.60$ μg mtDNA per g of tissue. The mean yield from fresh *S. aurita* gonads stored in MSB-$Ca^{++}$ for 7 days at 4°C was $1.18 \pm 0.45$ μg mtDNA per g of tissue. The semifresh *O. oglinum* processed after 5 days of storage yielded $1.01 \pm 0.66$ μg mtDNA per g of ovarian tissue. Isolation of mtDNA from material quick-frozen on liquid nitrogen was also achieved, but yields were reduced by as much as 56% from that of the semifresh samples.

Various concentrations of mtDNA were electrophoresed on Hoechst 33258/agarose gels. The minimum concentration required to produce clear, resolvable restriction fragments (at the 500-base pair (bp) level) was 11.8 ng/μL in 20-μL wells. Fragment mobilities from separate digestions with the two restriction endonucleases indicated the mtDNA genome size for *S. aurita* to be 16,263–16,353 bp, and that of *O. oglinum* to be 15,186–15,683 bp.

## Discussion

The techniques presented here have successfully addressed some of the potential problems associated with performing a large population study using mtDNA. Purification of sufficient quantities of mtDNA to perform a detailed restriction-site analysis has been

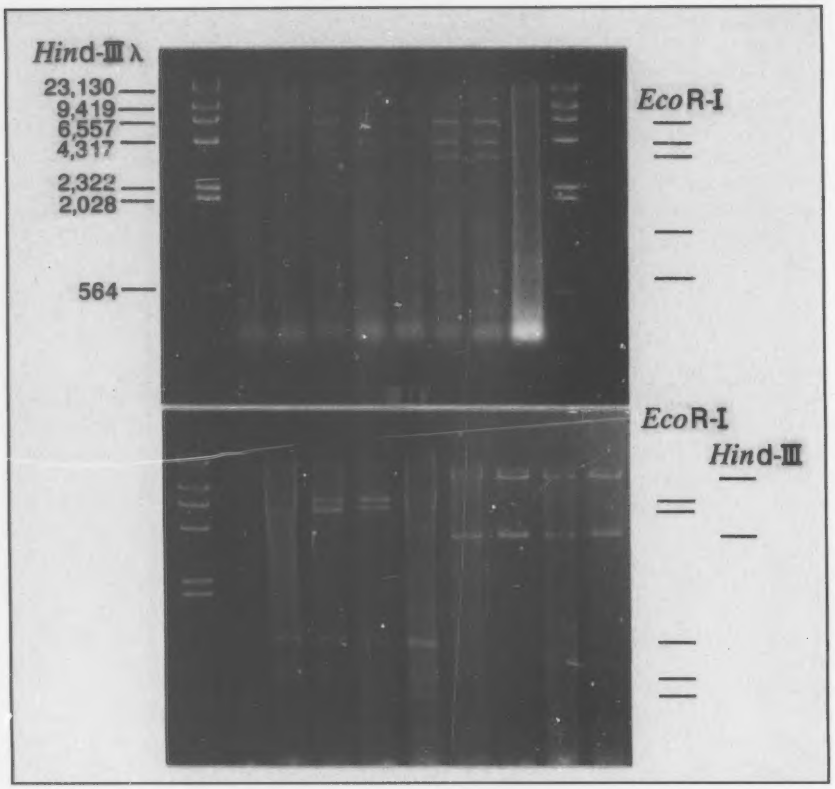


**Figure 2**
Top: Restriction digests with *Eco*-RI of mtDNA from Spanish sardine *Sardinella aurita* visualized on a routine Hoechst/agarose gel photographed in transilluminated UV light. Lane 1 is the *Hin*d-III digested λ-DNA standard. Bottom: *Eco*-RI (left) and *Hin*d-III digests of mtDNA of threadherring *Opisthonema oglinum*. All digests were carried out on ~0.3 μg of mtDNA for 2.5 hours, then electrophoresed for 3 hours at 50 volts. The *Hin*d-III digest of *S. aurita* mtDNA (not shown) produces five fragments compared with two for that of *O. oglinum*.

accomplished through low-volume density-gradient separation in a relatively inexpensive tabletop ultracentrifuge which is essentially portable. This simple overnight ultracentrifugation followed by extraction of the mtDNA and subsequent ethanol precipitation would allow mtDNA isolation from at least 30 individuals in a normal work-week by a single worker. Five grams of fresh, ripe, ovarian tissue should produce enough mtDNA per individual to be digested separately by 20 restriction endonucleases and still be resolved on Hoechst 33258/agarose gels.

Agarose gels incorporating the Hoechst 33258 fluorochrome (DeFlaun and Paul 1986) is a good substitute for staining of restriction fragments using ethidium bromide. Whereas Hoechst 33258 binds specifically and quantitatively to AT-rich mtDNA (Latt and Stetten 1976) ethidium bromide has mixed RNA-DNA specificity (Le Pecq and Paoletti 1966) reducing its resolving power and making visualization of small fragments (<500 bp) difficult. The suggestion of Lansman et al. (1981), that minimally 0.5 μg of mtDNA be used per digestion to insure visualization of fragments with ethidium-bromide staining, limits its resolving power to about 20 ng of DNA. In contrast, a zone of fragments containing only 7.0 ng of DNA (~1.8 μg per digestion) should be visible on Hoechst 33258/agarose gels, and these can be viewed immediately following electrophoresis on a UV transilluminator.

Our estimate of the sizes of the mtDNA genomes of *Sardinella aurita* and *Opisthonema oglinum* is close to those obtained for other clupeids (Kornfield and Bogdanowicz 1987, Avise et al. 1989). Ours are probably very good estimates since the pattern-recognition system used here greatly reduces measurement error of fragment mobility inherent in the use of stereomicroscopes and other manual methods. This survey of only a few individuals did not reveal any polymorphisms at *Eco*-RI or *Hin*d-III in either species, but the restriction fragments produced at both restriction sites are quite distinct between the species (Fig. 2). With new microextraction methods for mtDNA available (Graves et al. 1990), it should be possible to eventually separate or identify even the eggs and very young larvae of *S. aurita* and *O. oglinum* obtained in field samples. The ability to do so could be used to provide estimates of egg and larval mortality rates in the

earliest life-history stages of these and other important pelagic species.

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